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# II. Lucifer: *a Study in Morphology.*

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## Section I.—Introductory.

The general anatomy of the adult *Lucifer* has been satisfactorily made known by the observations of Souleyet, Huxley, Hensen, Dana, Semper, Claus, Dohrn, and Faxon; and the only facts which I have to add relate to the structure of the reproductive organs.

The earliest recorded observations upon this subject are by Dana ('United States Exploring Expedition during the Years 1838, 1839, 1840, 1841, and 1842,' under the Command of Charles Wilkes, U.S.N., vol. xiii., part 1). In plate 44, fig. 9, *b*, *h*, and *m″*, he gives a very correct representation of the male reproductive organs and spermatophore of an adult male specimen of *Lucifer* (*acestra*); but his description of these figures (p. 670) shows that he was completely at a loss for an interpretation of the parts which he has represented, and had no idea of their true function.

Later students have entirely overlooked these figures by Dana, and there has been

some doubt whether *Lucifer* is an adult animal at all, rather than the young form of some other Decapod.

In 1861, Semper (Reisebericht des Herrn Dr. Sempers. Ein Schreiben an A. Kölliker; Zeit. f. Wiss. Zool., xi., 1861, pp. 100–108) re-discovered and described the male organs, and also the female organs, of a large, transparent, and probably new species which he found at Zamboanga.

He gives no figures, and his short account, which is in the main correct, is as follows:—

"Die Geschlechtsöffnung ist einfach, liegt bei beiden Geschlechtern in der Mittellinie des Bauches, dicht hinter dem letzten Brustfusse. Der Hode besteht aus einer, in der Mittellinie des Thorax, dicht unter dem Magen liegenden Samendrüse, an deren hinteres Ende, dort wo der kurze Samenleiter entspringt, sich mehrere Nebendrüsen ansetzen. Der Same wird, noch unentwickelt, in einen birnförmigen grossen Spermatophor eingeschlossen. Das hinterste Ende dieser männlichen Drüse reicht bis in die Mitte des ersten Hinterleibgliedes, das vorderste bis ziemlich dicht an den Schlund.

"Das Weibchen hat zwei Eierstöcke, die vom Ende des sechsten Hinterleibgliedes an dicht unter dem Darm, sich bis in die Mitte des Thorax erstrecken, hier biegen sich die beiden Samenleiter nach unten, und schwellen dann zu zwei grossen Taschen an, die eine kleine Tasche umfassen; die Geschlechtsöffnung ist einfach; ein einziger Spermatophor steckt mit seinem spitzen Ende darin. Entwickelte Zoospermien habe ich nicht beobachtet. Weibliche Begattungsorgane fehlen. Die Entwickelungsgeschichte ist mir unbekannt geblieben."

The male organ has two external openings; they are not on the median line, and their position in the body does not correspond to that of the female orifice; but in other respects my own observations show the correctness of this description.

As Semper does not give any account of the general structure of these sexual individuals, Claus ("Ueber einige Schizopoden und niedere Malacostraken Messinas," Zeit. f. Wiss. Zool., xiii., 1863, pp. 433–437) held that the adult nature of *Lucifer* must still be a matter of uncertainty; but in 1871 Dohrn verified Semper's account from alcoholic specimens ("Untersuchungen über Bau und Entwickelung der Arthropoden," von Dr. Ant. Dohrn, Zeit. f. Wiss. Zool., xxi., 1871, p. 357), and showed that the mature animals have the form which had been described by Thompson ('Zoological Researches and Illustrations,' 1829, p. 58) as characteristic of the genus.

In the following year Semper ("Zoologische Aphorismen, von C. Semper: I. Einige Bemerkungen über die Gattung *Lucifer*," Zeit. f. Wiss. Zool., xxii., 1872, p. 305) published a second paper, in which he gave two good figures of the male and female reproductive organs (taf. xxii., figs. 3 and 4), but added nothing to his earlier description.

During my own studies upon the development of the larva I found an abundant supply of adult specimens of both sexes, and am thus enabled to give a more complete account of the structure and relations of the reproductive organs.

Plate 9, fig. 75, is a side view of the carapace (*c*) and the first abdominal

somite (*a*) of an adult male, showing the first abdominal foot (*Pl.* 1) and the basal joints of the third maxilliped (*Mp.* 3), and the first, second, and third thoracic limbs (*Pr.* 1, *Pr.* 2, *Pr.* 3). The testis (*t*) consists of a series of about eight pouches or follicles, which hang down into the body cavity under the anterior end of the intestine (*i*). The body of the animal is so thin that it is almost impossible to get a good dorsal view without crushing the specimen; but a very careful examination of the side view seems to show that there is only a single organ on the median line of the body, as SEMPER states. On each side of the intestine, along the line where the testis joins its wall, a small tubular vas deferens (*vd*) arises, and runs backwards along the side of the intestine nearly to the end of the first abdominal somite, to which it seems to be attached (at *l*) by a ligament. It then bends outwards and forwards upon itself to form a second much larger portion (*sp*), which is parallel to and outside of the first portion, and reaches nearly to the anterior edge of the first abdominal somite. The third or terminal portion (*sv*) has a large cavity, thick walls, and it runs down to an external opening which is situated on the outer edge of the sternal surface of the thoracic region, behind the basal joint of the third pereiopod, and therefore in the position which would be occupied by the basal joints of the fourth or fifth pereiopods if they were present.

There is a vas deferens, made up of these three portions, on each side of the body, and the ventral nerve chain (*tg*) passes between their external openings.

The more anterior follicles of the testis are almost perfectly transparent, but the development of the male cells in the posterior ones gives to them a faint granulation. The first division of the vas deferens (*vd*) has a small cavity, thin walls, and as it usually seems to be entirely empty it is probable that the passage of the male cells from the testis through it to the second division (*sp*) takes place quickly. The second division (*sp*) has a very large cavity, and in it the male cells become arranged in a single layer around the surface of a central core, which is formed of some dense transparent adhesive substance.

The spermatophore appears to pass into the third chamber (*sv*) before it is completely formed, as all those which were seen in the second chamber consisted only of a central core and a layer of male cells, while those which were contained in the thick-walled third chamber had an outer enveloping capsule.

I found several specimens with a fully-developed spermatophore on one side of the body and none on the other side, and was thus enabled to thoroughly satisfy myself of the presence of two vasa deferentia, and two external openings.

I was unable to discover how the spermatophore is transported to the body of the female, or what part the clasping organ (*c*) upon the first pleopod of the male performs during the act of copulation.

Upon several occasions I observed a male clinging to the basal joints of the first antennæ of a female, but as I never succeeded in getting the pair under a lens without separating them, I made no careful examination. Copulation usually takes place

during the daytime, or at least this was the case in every instance which I observed. In several cases I found female specimens with a single fresh spermatophore attached to the opening (Plate 9, fig. 74, *o*) of the seminal receptacle (*sr*). This opening is situated between and a little anterior to the basal joints of the third pair of thoracic limbs (*Pr.* 3 of fig. 74). As the spermatophore gradually discharged its contents, it was easy to see that both the central core and the investing layer of spermatozoa escaped from the outer sheath and passed into the seminal receptacle. In all the breeding females which I observed the spermatozoa filled the posterior, and the transparent core of the spermatophore the anterior half of the spermatic receptacle, as shown in fig. 74. The ovary is very long (fig. 74, *ov*), and it lies under the intestine, reaching from the fifth abdominal somite to the posterior edge of the carapace, where it bends upon itself at right angles and runs down to its external opening, which is upon or close to the median line of the ventral surface, a little in front of the third pair of pereiopods. The wall of the ovary is so very thin and delicate that I was not able to detect it at all except when it was filled with ripe ova. These are very much elongated, granular, and slightly opaque; and there does not seem to be any shell around them. They are very elastic, and undergo great changes of shape as they pass through the small oviduct.

Oviposition occurs between 9 and 10 o'clock in the evening, and occupies only a few minutes.

After the eggs are laid they are spherical, transparent, and each one has a rather thick shell. They are attached, in a loose bunch of twenty or more, to the last pair of thoracic limbs, and in order to save space I have shown them in fig. 74, although the specimen from which the figure was drawn had not laid any of its eggs.

As I obtained very few ripe females, I was not able to sacrifice one of them to study the reproductive organs under pressure, and I am therefore unable to decide whether any parts of this system are double; but I feel confident that there is only one spermatic receptacle, and the opening of the oviduct seems to be upon the median line.

We found a few adult specimens out at sea, but, while I was able to learn little about their habits, I think that they are not strictly pelagic, but that their proper home is the salt marshes close to the ocean.

They were met with in the greatest abundance about half-a-mile inside Old Topsail Inlet, near a large marsh, during the first hour of the ebb tide, on calm evenings when the tide turned between 7 and 8 P.M.; and I infer that they leave the marshes at this time to breed in the ocean. All the mature females which we found, with one exception, were captured under these peculiar conditions; and we never failed to find them at this spot when the tide turned about sunset and the water was calm.

Owing to this singular limitation there are only a very few favourable evenings for procuring the eggs in a single season; and until the animals can be made to thrive and multiply in confinement, it must always remain an extremely difficult matter to procure the eggs in abundance.

Up to the present time our knowledge of the early stages of *Lucifer* has been extremely meagre.

In his report on the Crustacea of the United States Exploring Expedition, DANA described (p. 634) an organism under the name of *Erichthina demissa*, and figured it in plate 42, fig. 3. CLAUS ('Crustacean System,' p. 13) gives a figure of the same organism at a latter stage of development, and calls attention to the numerous features of resemblance to the *Protozoëa* stage of development of *Penæus*.

Only a few months before his death, the lamented WILLEMÖES-SUHM collected a number of specimens of *Erichthina* in the South Pacific, and, associated with them, a sufficient number of later stages to assure him that *Erichthina* is the larva of *Lucifer*. His account ("Preliminary Remarks on the Development of some Pelagic Decapods," by R. von WILLEMÖES-SUHM, Ph.D., Proc. Royal Soc., Dec. 9, 1875, p. 132–4) is very brief, and as it contains all that is known about the metamorphosis of this extremely interesting form, I quote it in full :—

"Very similar to that of *Sergestes* is the development of *Leucifer*. Here the earliest *Zoëa* of a species from the Western Pacific has got at first no eyes, then sessile ones came out, and the animal then presents the form which DANA has called *Erichthina demissa*, and which CLAUS suspected to be not a Stomatopod but a Schizopod larva. After the second moulting this *Erichthina* gets stalked eyes, and very long setæ on all its appendages, becoming a rather long, very delicate *Zoëa*. It now enters the *Amphion* stage, but never gets more than four pairs of pereiopods, and loses another pair of these when it moults for the youngest *Leucifer* stage, in which two pairs of pereiopods are absent.

"The next question after having found this out, was, of course, whether *Amphion*, *Sergestes*, and *Leucifer* leave the egg as a *Zoëa*, or whether there is a preceding *Nauplius* stage. My own impression is that in the two first-named genera this is not the case, as the youngest *Zoëas* which I caught had all the same size, and as none of them was without the large lateral stalked eyes. As for *Leucifer*, the question appears to me to be doubtful; for it is, from what I have seen, quite possible that my youngest *Zoëa*, which has only got a central eye, may be preceded by a *Nauplius*. Of course, the simplest thing would be to get the eggs; but there is the difficulty, for *Amphion* is caught very rarely, and has never been obtained at any other time but between 8 and 12 P.M., when it is extremely difficult by lamplight to find out the youngest stages. *Sergestes* larvæ are commoner, appearing also in the daytime, and *Leucifer* is sometimes caught in abundance. I hope, therefore, that I shall succeed in completing my researches about this question, especially as far as the two latter genera are concerned.

"H.M.S. 'Challenger,' Honolulu, Sandwich Islands.

"July 30, 1875."

As the sad death of this lamented naturalist, only a short time after, put an end to this as well as to his other researches in all departments of zoology, I take pleasure in

stating that I have fortunately been able to complete his observations upon *Lucifer*, and to furnish a very perfect account of its entire metamorphosis, as well as a few important facts with reference to its development in the egg.

At the end of April, 1880, I found a single specimen of *Lucifer* with two eggs attached to one of its appendages, and I was led by the great importance and interest of the subject to make every effort to trace its life-history. For four months I met with no success whatever, but about the 1st of September I found a few advanced larvæ, and traced them to the adult, and I then succeeded in finding earlier stages and tracing them as far as the stages which I had previously found, but it was not until the last week of my season at the sea-shore that I succeeded in hatching the *Nauplius* from the egg, and the last gap in my series was bridged by a moult which occurred only a few hours before my departure.

As the result of my four months' efforts I can now state that I have seen the eggs of *Lucifer* pass out of the oviduct. I have seen the *Nauplius* embryo escape from the same egg which I had seen laid, and I have traced every moult from the *Nauplius* to the adult in isolated specimens. There is therefore no Crustacean with the metamorphosis of which we are more thoroughly acquainted than we now are with that of this extremely interesting genus.

Not only is it true, as Willemöes-Suhm has pointed out, than Dana's *Erichthina demissa* is a larval stage of *Lucifer*, but that Dana's *Sceletina armata* is a later stage in the same series, while some of the forms which he includes in his genus *Fureilia* are also, in all probability, *Lucifer* larvæ.

The occurrence of a free *Nauplius* stage of development in the life-history of one of the higher Crustacea is a matter of such profound significance in the scientific discussion of the phenomena of embryology in general, that it can hardly be accepted without question so long as there is any possibility of error. Two of the observers who have testified to its occurrence have based their conclusions upon evidence which would be perfectly satisfactory in any ordinary case, but as they did not actually trace all the stages of development their statements do not stand the severe analysis which the importance of the case demands, and certain naturalists have therefore refused to give them unqualified acceptance.

The third observation was made so many years ago, and the larva is so briefly described, that it would not be safe to assume, in the absence of all corroborative evidence, that it is a *Nauplius* at all.

In December, 1838, Dana found in the harbour of Rio de Janeiro great numbers of specimens of a Schizopod, which he described ('United States Exploring Expedition during the Years 1838-1842,' under the command of Charles Wilkes, U.S.N., vol. xiii., part i., p. 654) as *Macromysis gracilis*. In the brood-pouches of some of his specimens he found an abundance of eggs and developing embryos, several of which are shown in his plate 45, fig. 5. He made no careful study of their structure; his notice of them in the text is only a few words; and his figures are very small,

and show the embryos in dorsal view, as seen under a very low magnifying power, but they are so much like FRITZ MÜLLER's figures, that we must acknowledge that the credit of the first discovery of a Malacostracan *Nauplius* belongs to DANA, and that up to the present time this is the only case in which a *Nauplius* has been traced to an egg which could be definitely identified as that of a specific adult Malacostracan, although his account is so imperfect that in itself it is certainly not sufficient to prove the existence of the *Nauplius* stage at all.

In 1861 FRITZ MÜLLER found, at Desterro, in Brazil, a single specimen of a *Nauplius* ("Die Verwandlung der Garneelen." Erster Beitrag von FRITZ MÜLLER, in Desterro, Arch. f. Naturgeschichte, 1863, p. 9), which he traced, through other specimens which were also collected in the ocean, to a form which he believed to change into the youngest *Zoëa* of a species of *Penæus*. The series of stages is so satisfactory that there is no reason for doubting the accuracy of his conclusion, but the chances for error, in the attempt to trace Crustacean development from isolated specimens, are so very great that the statement has not received unqualified acceptance.

The only other recorded observation of a Malacostracan *Nauplius* is not among the Decapods, but in the more embryonic Schizopods. These observations, which were made by METSCHNICKOFF, would tend to corroborate those by MÜLLER, but they are unfortunately open to the same criticism. He did not actually rear the larvæ and trace them to a specific adult, and although there would in ordinary cases be no doubt of the correctness of his conclusion, a careful analysis of his papers will show that there certainly is a possibility of error.

In the spring of 1868 he collected from the surface of the ocean at Messina a few early stages in the development of a Crustacean, which he believed to be *Euphausia mulleri* (CLAUS), and showed ("Ueber ein Larvenstadium von *Euphausia*" von EL. METSCHNICKOFF in Petersburg, Zeit. f. Wiss. Zool., xxix., 1869, p. 479, taf. xxxvi.) that it passes through a well-marked *Nauplius* stage, of which he gives three figures.

The following year, at Villafranca, he collected a good supply of young larvæ and floating eggs in advanced stages of development, and was thus enabled to supplement his first paper by a second ("Ueber die Naupliuszustände von *Euphausia*," von ELIAS METSCHNICKOFF, Zeit. f. Wiss. Zool., xxi., 1870, p. 380, taf. xxxiv.) in which he gives a minute account of the *Nauplius* from the time it leaves the egg until it changes into a form somewhat similar to the youngest stage of *Euphausia*, which had been previously described by CLAUS ("Ueber einige Schizopoden und niedere Malacostraken Messinas," von Prof. Dr. C. CLAUS, Zeit. f. Wiss. Zool., xiii., 1863, p. 422). CLAUS had supposed this to be the stage in which the larva leaves the egg, and he says (p. 450), "Diese Larve bin ich geneigt für die jüngste aller freieren Entwickelungsformen der *Euphausia* anzusehen." He subsequently learned, however ("Untersuchungen zur Erforschung der Genealogischen Grundlage des Crustacean-Systems," p. 9), that he had been in error, since he afterwards found, in an Atlantic and also in a Mediterranean species, an earlier *Protozoëa* stage, which changed into the *Zoëa* described in his first paper. It therefore

follows that METSCHNICKOFF studied something else, or that he was in error in believing that he had traced his *Nauplius* directly to what CLAUS has shown to be a somewhat late stage in the development of *Euphausia*. METSCHNICKOFF's only reason for believing that his *Nauplius* is a young *Euphausia* is its resemblance to CLAUS's larva, and as there is certainly an error here, we are not justified in giving unqualified acceptance to his statement that it is an *Euphausia* larva. It seems very probable, indeed, that this is the case, but in the absence of the direct evidence which could only be afforded by actually tracing it back to an *Euphausia* egg, or forwards to the adult *Euphausia*, I do not think that the existence of a Malacostracan *Nauplius* can be said to be established by these observations, for they do not stand the severe test which is demanded by their unusual importance, and I think the facts justify the statement that, up to the present time, there has been no unquestionable evidence of the occurrence of such a stage of development in the higher Crustacea.

The present series of observations is complete at both ends, and I have not relied upon surface-collecting to fill a single gap, but have traced every stage in isolated captive specimens, and the possibility of error seems to be entirely out of the question.

The close resemblance between the *Nauplius* of *Lucifer*, and MÜLLER's and METSCHNICKOFF's larvæ, renders it almost certain that they also are Malacostracan larvæ, but before this corroborative evidence was furnished, it was certainly quite possible, although hardly reasonable, to doubt whether this was true of either of them.

## II.—The Segmentation of the Egg, and Formation of the Food-yolk and Primitive Digestive Cavity.

Unusual difficulties attend the study of the early stages in the embryology of *Lucifer*, and the observations which I have been able to make are incomplete, and leave many gaps to be filled and many interesting points to be decided by future investigations; but the facts which I have made out are so novel, so different from all that was previously known of the early stages of Arthropod development, and they throw so much light upon the relation of the peculiar and greatly modified form of segmentation characteristic of the group to the less modified form of segmentation presented by the more normal eggs of other animals, that it seems best to give my results in their present incomplete state.

I am the more willing to do this, because the peculiar difficulties of the subject leave little hope for the attainment of more complete results in the future.

The eggs are so loosely attached to the appendages of the female that they are broken off by the slightest roughness of handling, and it is very difficult to obtain them by collecting the egg-bearing females. Even when great numbers of mature specimens are captured in the breeding season, with the greatest care and delicacy, very few of

them, much less than 1 per cent., are found to have eggs attached to their limbs when the collection is examined.

If the mature animals could be induced to thrive and multiply in confinement, there would be no difficulty in obtaining a sufficient supply of eggs, but until this can be done it must be extremely difficult to procure them in sufficient numbers for exhaustive study.

During the early stages the eggs are so delicate that they are soon destroyed by the confinement and compression to which it is necessary to subject them while they are under examination, and it is therefore impossible to watch very many stages in a single egg.

When we add to this that the eggs are laid about 9 o'clock in the evening, and must be studied between this time and daylight, after several hours of laborious collecting, by eyes that have been already severely taxed with looking over the collections and picking out the transparent and almost invisible adults by an artificial light, and examining each one of them with a lens to find those which carry eggs, the difficulty of the subject will be appreciated.

The eggs are spherical, transparent, and they contain extremely little food-material. This is uniformly distributed over the whole egg in minute globules, which have nearly the same colour and refractive index as the surrounding protoplasm.

The egg undergoes total regular segmentation, and a true segmentation cavity occupies the place filled by the large central yolk-mass in the eggs of other Arthropods.

It first divides into two equal portions (Plate 1, fig. 1); then, by a cleavage at right angles to the first, into four (fig. 5); then into eight (fig. 8); then into sixteen (fig. 10); and so on.

At the stage shown in fig. 10 the inner ends of the sixteen spherules are seen to be separated from each other by a central space, the segmentation cavity, which persists, and is shown at later stages in figs. 11, 13, 15, 16, 17, 19, and 20, at *b*.

In fig. 10 the egg will be seen to be spherical, and all the segments have their broad ends at the surface; but in the next stage one pole of the egg becomes a little flattened, and in an optical section the spherule (*c*), which occupies the centre of the flattened area, is seen to have its broad end nearest the centre of the egg.

Most of the food-material has meanwhile disappeared from the other spherules, which are now quite transparent, while the spherule (*c*) still contains as much as ever, but apparently no more than there was contained at an earlier stage in an equal area of any part of the egg. In an optical section of the same egg, in a plane at right angles to that of fig. 11, the spherule (*c*) shows a trace of a fissure, which a little later divides it into two (see fig. 12, *c*).

Plate 2, fig. 13, is an optical section, like the one given in fig. 11, of a somewhat older egg; and fig. 14 an optical section of the same egg at right angles to fig. 13. The outline is a little more flattened on one side than it is in fig. 11, and the

spherule (*c*) is completely divided by a radial fissure into two, and these project into the segmentation cavity (*b*) a little more than they did before.

In fig. 15 the flattening has become a deep pit (*d*), and the spherules (*c*) have been pushed quite into the segmentation cavity, and the adjacent cells have begun to move in the same direction. This change is more marked in fig. 16; and in fig. 17 the egg consists of a double wall of cells, the ectoderm and the endoderm, surrounding a primitive digestive cavity (*d*), and separated from each other by the segmentation cavity (*b*), in which the two cells (*c*) are situated. Each of these also shows traces of a division into two.

These changes are more marked in fig. 19; and in fig. 20 the opening of the primitive digestive cavity is much reduced in size, and the cavity itself does not lie exactly in the axis of the egg, but at one side of it.

A more minute examination of the segmentation brings out a number of interesting points; one of them is the rhythmical character of the process, which is not a continuous uniform change, but a series of stages of activity, separated from each other by periods of rest.

The egg shown in Plate 1, fig. 1, was laid about 10 o'clock P.M., and about 10.35 it was in the condition which is represented in the figure. As I had not been watching it I did not observe the first division, and when first seen it was in the resting condition, and the two spherules were not sharply defined, but pressed together.

During the next fifteen minutes no external change was visible, and the drawing was made at 10.50 P.M. It then entered upon the second period of segmenting activity, and in five minutes the two spherules were well defined, as shown in fig. 2; and in five minutes more (fig. 3) one of them showed traces of division into two. In ten minutes more (fig. 4) this division was completed, and traces of a similar change had made their appearance in the other spherule, which was also perfectly divided into two at the end of five minutes more (fig. 5). This stage ended the second period of activity, which was twenty-five minutes long.

During the whole of this time the egg showed gradual and uniform change, which was sufficiently rapid to be distinctly visible. Although four so-called stages are figured, there was no division into stages, but a continuous change without interruption.

The four spherules now began to flatten down, and in five minutes the egg was in the condition which is shown in fig. 6, and it then remained without any external change for more than ten minutes. The second period of rest, measured from the time when the four spherules began to shrink together to the time when they began to swell out and enter upon the third period of active segmentation, was therefore more than fifteen minutes long.

At 11.40 the four spherules were once more sharply defined (fig. 7), and changes went on uniformly until, at 12.15 A.M., each was perfectly divided into two, as shown in fig. 8, which marks the end of the third period of activity, thirty-five minutes long.

I was not able to watch this egg pass into the next resting stage, as it had been so

long under observation (1 hour 45 minutes) that its development was arrested at this point; but another egg in this stage of development was seen to pass into the resting condition, as shown in fig. 9, and it then remained quiet for about fifteen minutes, showing no external indications of change during this time.

At the end of the third period of rest the spherules again became prominent, so that the outline of the egg was exactly like that of fig. 8, and the egg entered upon the fourth period of activity, soon dividing into sixteen spherules (fig. 10), arranged around a segmentation cavity.

In about twenty-five minutes from the beginning of this period of activity the spherules began to flatten down once more, and the egg passed into the fourth resting stage, but it was not observed beyond this point.

The alternation of activity with rest was observed at much later stages, but after the gastrula invagination makes its appearance the cells of the endodermic portion of the egg do not undergo active change at the same time with those of the ectoderm, and the egg has one set of periods of activity for each layer. As development goes on the periods of rest grow longer and the periods of activity shorter, and the spherules do not flatten down while at rest.

The egg which is shown in optical longitudinal section in fig. 16 was in the field of the microscope for nearly twenty minutes, while I was examining another specimen. An occasional look at it showed that it was not changing, but at the end of this time I noticed that the outer ends of the ectoderm cells directly opposite the orifice of invagination were notched, as is shown in the figure. Activity spread in all directions from this point, and in less than five minutes all the cells were notched, and those nearest the centre of the area of activity were perfectly divided into halves. In about five minutes more all the ectodermal cells had divided, and this layer had the appearance shown in fig. 17—which, however, was drawn from another specimen.

This last egg remained in the condition shown in the drawing for fifteen minutes from the time it was first observed, and a movement of the appendage to which it was fastened caused it to roll over and present its formative pole for examination before the beginning of the next period of activity, which is shown in surface view in fig. 18. The manner of division was simply a repetition of that which has just been described.

The cells nearest the centre of the formative area became notched, and then divided into halves; and the activity gradually spread over the egg in all directions, until, in a few minutes, all the cells which were visible were at some stage of division.

The rapidity and uniformity with which this change spread over the egg rendered it an extremely interesting and impressive sight, and I know of no other case in which segmentation is so perfectly regular at such an advanced stage of development.

The activity did not affect the endoderm cells in either of these cases, but at a later stage (fig. 20) they were seen to be in an active segmenting condition at a time when the ectoderm cells were at rest. I was not able to keep this egg alive long enough to watch the completion of the process, for it had been under the microscope for some

time before the stage shown in the figure was reached; but the division of the endoderm cells appears to go on much more slowly than that of the ectoderm cells.

This phenomenon, the alternation of periods of rest with the periods of active segmentation, does not seem to have received from embryologists the attention which it deserves. A number of observers have pointed out that in many animals, among the Mollusca especially, the distinctness of the spherules becomes more or less completely obscured after each division, and that this state persists until just before the next division, when the spherules swell out and again become conspicuous. The change of form does not seem to be at all general, and in most accounts of segmentation nothing of the kind is recorded.

I believe that it is a secondary phenomenon, and that the essential thing is the alternation of rest with activity; and I am confident that careful time records of segmentation will show that this occurs in nearly every case, sometimes with and sometimes without the accompanying change of form.

I have observed it in *Physa*, *Limnæus*, and *Planorbis*, where segmentation is total and nearly regular; in the Oyster, where the egg has a rudimentary food-yolk and segmentation is irregular; in a bony fish with a large food-yolk and a discoidal segmentation; and in *Lucifer*. Other investigators working under my guidance have observed it in *Amblystoma* and in oligochætous and polychætous Annelids. These are all the cases in which I have been able to test the matter since my attention has been attracted to the subject; and as the alternation was found to occur in every case, although the animals are so widely separated and present such diverse modes of segmentation, I feel justified in assuming that the phenomenon is general, and will be found in all eggs which can be properly examined by watching and timing them while segmentation is going on.

The cause of rhythmical physiological change is an extremely interesting question; and as the segmenting egg exhibits the phenomenon in the greatest possible simplicity, it would seem to be a peculiarly favourable subject for investigation.

The phenomena which have been described seem to show that segmentation is not due to the action of any purely molecular force, like polarity, but is essentially a vital activity, and in a paper on the embryology of the fresh-water *Pulmonates* ('Studies from the Biological Laboratory of the Johns Hopkins University,' vol. i., part ii.) I have ventured the following explanation.

During the period of segmentation the protoplasm of the whole egg (of *Physa*) gradually becomes more and more transparent, on account of the gradual disappearance of the granular food-material which it contains, and the rhythmical character of the process of segmentation would seem to admit of a simple explanation on the supposition that the physical properties of the protoplasm offer a resistance which must be overcome before the force which is set free by the assimilation and reduction of the food-material can exert itself to bring about the active changes of segmentation. During a period of rest the process of digestion and assimilation accumulates a store

of energy which, at length, becomes sufficient to overcome this resistance, and to initiate a period of activity which lasts until the whole of this reserve of force has been expended in the rearrangement of the protoplasm. The physical properties of the protoplasm now reassert themselves, and tend to reduce the whole egg as nearly as possible to a spherical form once more, and the egg then remains inactive until the supply of energy again becomes great enough to overcome the resistance.

If this is the true explanation we should expect to find the alternation of rest and activity much more general than the change of form, for the degree of consistency of the protoplasm or the amount or character of the food-material, or the way in which it is distributed through the egg, may prevent the second set of changes from showing themselves. This is precisely what we do find, and in the bony fishes, where the large food-yolk would prevent any marked change of form, we find the first set of changes well marked, but with no trace of the second set.

Leaving this subject for the present, I wish to say a few words about another interesting phase of the early stages of *Lucifer*. We cannot fail to be impressed by the very remarkable departure from ordinary Arthropod segmentation, nor can we overlook the fact that in all the points of difference from the eggs of allied forms, the eggs of *Lucifer* show a most suggestive resemblance to the ordinary unspecialized ova of other Metazoa.

In an ordinary Arthropodan egg we have, as the outcome of the process of segmentation, a central mass of food-yolk, which may or may not be divided into segmentation products, and which completely fills the segmentation cavity; and an outer investing layer of blastoderm cells; that is, the egg undergoes a centrolycethal segmentation.*

In most Crustacea the early stages of segmentation are regular, and apparently total, but the lines of cleavage do not pass entirely through the egg, and the spherules are united to each other by a central mass of food-yolk. When segmentation is somewhat advanced the products of segmentation become more or less pyramidal, with the bases of the pyramids at the surface, and their apices fused together at the centre of the egg. The outer ends of the pyramids then become transparent and separate off as a blastoderm, while the inner portions usually fuse together, more or less perfectly, to form a central food-yolk, which fills the space which in ordinary eggs constitutes the segmentation cavity. A small portion of the blastoderm then becomes invaginated to form the primitive digestion cavity, and the remainder becomes the ectoderm.

The centrolycethal type of segmentation presents great variations in the different groups of Arthropods, but in nearly all cases its peculiarities are so well marked

* The whole subject of segmentation has been so ably and exhaustively reviewed by Balfour in his recent work on 'Comparative Embryology,' that it does not seem necessary to burden this paper with a long list of references to the literature of Arthropod segmentation, or to enter into an exposition of the present state of our knowledge of the subject. All the essential facts and opinions may be found on pages 79–99, 317–379, and 425–433 of vol. i. of the 'Comparative Embryology.'

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that it is difficult to trace any resemblance to the various forms of segmentation which occur in other groups of animals. In *Lucifer* the case is reversed, and we have a type of segmentation which is obviously similar to that of the Echinoderms, Annelids, Molluscs, Tunicates, Vertebrates, &c., but is less obviously related to that of the eggs of closely allied forms. The resemblance to what may be called "normal" segmentation is so plain that it need not be dwelt upon, but the relation between the egg of *Lucifer* and an ordinary centrolycethal egg is by no means clear.

It seems probable, however, that since the food-material which has not been assimilated becomes centralised, after segmentation is somewhat advanced, in the single spherule *c*, of fig. 11, this spherule must correspond to one of the yolk-pyramids of an ordinary Crustacean egg. This then divides, by radial fission, into two portions (fig. 13, *c*), and it seems probable that the food-material then becomes restricted to their central ends, while the outer protoplasmic ends separate off as a pair of blastoderm cells (fig. 15), thus leaving the two masses of food-yolk (*c*) inside the segmentation cavity. While I was investigating the subject I regarded the spherule *c*, of fig. 11, as a primary mesoblast, which became pushed into the segmentation cavity, and then divided up to form the mesoderm; and I expressed this view without comment in a preliminary abstract of the subject ("Embryology and Metamorphosis of the Sergestidæ," Zoologischer Anzeiger, iii., p. 563). In most cases where the origin of the mesoderm has been most carefully studied, it originates by the separation of the inner ends of the cells which are to give rise to the endoderm, either before or during or after the invagination takes place; the mode of origin of these spherules in *Lucifer* and their position in the egg agree with what we should expect if they belong to the mesoderm, but the great quantity of food-material which they contain would hardly be looked for in this case, and favours the view that they are yolk-pyramids rather than mesoblasts.

As I examined no eggs between fig. 20 and fig. 21, the later history is uncertain, but a reference to figs. 21, 22, 23, and 24, which are about twenty hours later than fig. 20, shows that the region of the digestive tract of the *Nauplius* is marked by the presence of a number of large polygonal masses of what appears to be food-yolk, and it seems probable that these are the derivatives of the spherules *c*, of fig. 20. I was not able to actually witness the change from fig. 11 to fig. 15, and cannot state with absolute certainty that the spherules *c* divide into a central and a peripheral portion. Fig. 15 seems to indicate that this is the case, but in the absence of direct observation of the change, it is possible that the two cells which in fig. 15 lie below the cells *c*, are the ones which were at its sides in fig. 11.

If each of the cells *c* gives rise to a blastoderm cell, we should expect to find two more cells in fig. 15 than in fig. 18, but the number is the same. This is hardly a safe guide, however, for while the drawings are careful copies from Nature, they are not from the same egg, and the cells are so wedged together that vertical sections in

different planes would not intersect the same number in all cases, and there may have been two more in fig. 15 than in fig. 13.

I think, then, that the facts indicate that *c* of fig. 11 is a yolk-pyramid, rather than a primary mesoblast, and that after it divides into two, as in fig. 13, each part gives rise to a central portion *c*, and a peripheral endoderm cell.

If we accept this view and regard the cell *c* as a yolk-pyramid, two views as to the relationship between the egg of *Lucifer* and an ordinary Crustacean egg at once suggest themselves.

We may hold that *Lucifer* presents the primitive or ancestral form of segmentation, of which centrolycethal segmentation is a secondary modification. In this case we may suppose that as the supply of food-material gradually increased, new food-bearing cells or yolk-pyramids were added until all the cells were included, and the segmentation cavity was entirely filled and obliterated by them.

According to the other view, we may hold that the segmentation of the *Lucifer* egg is a secondary modification, which has been brought about by the gradual reduction of the amount of food-material, and its restriction, at last, to a single one of the cells of the segmenting egg.

There does not seem to be much difficulty in deciding which of these views is most satisfactory and probable. *Lucifer* is undoubtedly a very primitive Malacostracan, but it can hardly be regarded as a primitive Crustacean ; and the occurrence of perfectly centrolycethic segmentation in the Copopods, Phyllopods, Amphipods, and Isopods, as well as in the Decapods—forms below as well as forms above *Lucifer*—forbids us to believe that the egg of *Lucifer* is ancestral, or the unmodified descendant of an ancestral type of egg ; and we must therefore believe that the egg of *Lucifer* has been simplified by the loss of the greater part of its food-yolk.

A change of this kind is not without a parallel, and I have shown ("The Acquisition and Loss of a Food-Yolk in Molluscan Eggs," 'Studies from the Biological Laboratory of the Johns Hopkins University,' vol. i., part iv.) that the resemblance between the segmenting egg of the Oyster and a Molluscan egg with a food-yolk can only be explained by the supposition that the Lamellibranchs have inherited a rudimentary food-yolk which was functional at some past time, and that the assumption gives an explanation of all the peculiarities of oyster segmentation.

If we accept this view, and regard the egg of *Lucifer* as simplified by secondary change, it is extremely instructive to note that the loss of a food-yolk has brought it back to a type of segmentation which is directly comparable with that of ordinary Metazoan eggs, and we must therefore believe that a segmentation cavity is potentially present in all centrolycethic eggs, or else that the segmentation cavity of the egg of *Lucifer* is not homologous with that of ordinary eggs.

## III.—General Account of the Metamorphosis of Lucifer.

The most instructive method of studying the metamorphosis of *Lucifer* is to trace each part of the body through the series of changes which it undergoes from its first appearance until it assumes the adult form; but as this method of comparing the successive stages in the development of each organ necessarily involves references to other organs, it seems best to give first a general account of the whole structure of the larva at each stage of development, and afterwards to go over the same ground more rapidly in a different way, and to trace the history of each appendage.

### *The egg* Nauplius.

About thirty hours after oviposition the eye spot and appendages of the *Nauplius* became visible inside the egg-shell, as shown in a ventral view in Plate 2, fig. 21, and in a dorsal view in fig. 22. If the egg-shell is torn at this stage the embryo escapes, and swims about quite vigorously for a short time, but soon dies. The various parts of the body are much better shown in the swimming embryo than while it is contained in the egg, and I therefore give, for comparison with figs. 21 and 22, a dorsal view (fig. 23) and a ventral view (fig. 24) of an embryo which has thus been set free.

Fig. 23 shows an embryo of exactly the same age as those in figs. 21 and 22, while fig. 24 was drawn from an embryo a few hours older. The difference in the outline of the body is not due to this difference in age, however, but to a slight change in the point of view. In all four figures the letter *e* marks the anterior end of the body, and fig. 22 is a view directly opposite to fig. 21. Fig. 23 is in the same position as fig. 22, but the embryo shown in fig. 24 was in such a position that more of the anterior surface and less of the posterior surface was visible than in the other figures.

On the median line of the ventral surface the labrum (figs. 21 and 24, *L*) is very conspicuous at the anterior end of the body, and behind it there is a double row of four pairs of bud-like eminences, arranged in a longitudinal series. The first pair (figs. 21 and 24, *g*) are much larger than the others, and the depression which separates them on the median line is less marked than it is in the three pairs which lie behind. It is rather difficult to decide with certainty what this pair of buds becomes, but in the larva which Metschnickoff studied the changes were more gradual than they are in *Lucifer*, and he was therefore able to trace their history more satisfactorily, and to show that they become the metastoma. Their position with reference to other parts indicates that they have the same history here, and that the other three pairs of buds are the first and second maxillæ and the first pair of maxillipeds (*Mx.* 1, *Mx.* 2, and *Mp.* 1).

Three pairs of much larger appendages are folded down on to the sides of the body, within the egg; and when the embryo is set free they are seen to be the first antennæ

(*A*), the second antennæ (*An*), and the mandibles (*M*). They are not divided into joints or rings, although the second antennæ and the mandibles are biramous, and consist of a basal portion or protopodite, an expodite, and an endopodite. All three pairs have hairs projecting from their tips, and these lengthen considerably within a few minutes after the embryo is freed from the egg. The first antennæ are nearly as long as the second, and both pairs, as well as the mandibles, are organs of locomotion, to row the animal through the water. The motions of the larva are very erratic and violent, and consist of a series of quick leaps produced by vigorous backward strokes of the appendages.

The outline of the body will be understood by a reference to the figures. When the second maxillæ are in the centre of the field of view, as in fig. 21, the outline is pear-shaped, with the broad end of the pear at the posterior end of the body; but when the metastoma is in the centre this is reversed, and the broad end is in front. This difference is due to the fact that the dorsal region is much wider than the labrum and series of buds, which together form a ridge along the ventral surface.

In a dorsal view the simple eye (*Oc*) is seen as a black spot on the middle line, near the anterior end of the body. It did not show any traces of a division into halves at any stage of development which was observed.

The ocellus lies upon a large rounded granular body, which is imperfectly divided into halves by a notch upon its posterior margin. This body consists of the fused cerebral ganglia.

The dorsal portion of the posterior region of the body is swollen and rounded, as shown in figs. 21 and 23; and near its lateral margins there are a pair of small, but very conspicuous, dark pigment-spots (*i*), which might easily be mistaken at this stage for ocelli, since they have almost exactly the same size and colour. These two pigment-spots are very conspicuous during all the early stages of the metamorphosis, and their position during the later stages (figs. 25, 26, 27, 34, 35, and 47, *p*) shows that the portion of the *Nauplius* body which bears them becomes the thoracic, not the abdominal, region of the adult.

In the interior of the enlarged posterior portion of the body there is a huge mass of polygonal highly-refractive bodies, which appear to constitute a food-yolk, and which surround the digestive tract of the embryo. I have already given my reasons for believing that those bodies are derived from the spherule which becomes pushed into the segmentation cavity during the early stages of development. If this is their origin they must increase in size between the stage shown in fig. 20 and that shown in fig. 21. This is not at all an unusual occurrence, and in the fresh-water Pulmonates the yolk-spherules which surround the digestive tract continue to grow until a very advanced stage of development. I found so few eggs at this stage that I was afraid to sacrifice any of them by attempting to study their internal structure under pressure, and I am not able to give an account of the digestive tract or of the other internal organs.

When the embryo is set free from the egg it is seen to be inclosed by a delicate cuticle, which is shown, around the antennæ, in figs. 23 and 24. It is soon stripped off by the vigorous movements of the larva, and in fig. 24 it has been torn from all the appendages except the first antennæ (*A*).

In a dorsal view a number of muscular fibres are seen to extend outwards and forwards from the median line of the body to the basal joints of the antennæ.

The posterior end of the body is not notched, the anus is absent, and there is no trace of the telson or of the carapace.

### *The first free* Nauplius *stage.*

About thirty-six hours after oviposition the larva escapes from the egg as a *Nauplius*, $\frac{8}{1000}$ inch long, which is shown in side view in Plate 3, fig. 25. There is now no difficulty in keeping it alive and rearing it, and it swims very actively by vigorous strokes of its two pairs of antennæ. Its movements are very characteristic, and much like those of a Copepod or Cirrhiped *Nauplius*.

The most important differences between it and the egg *Nauplius* are the segmentation of the locomotor appendages, the lengthening of their hairs, the increased size and dendritic form of the pigment-spots (*p*), and the appearance of the telson (*Tl*), as a projecting fold furnished with two pairs of short spines or hairs, in the ventral surface of the posterior end of the body.

As regards the more minute structure of the appendages, the first antennæ (fig. 25, *A*) are five-jointed, and the hairs, which are more than half as long as the limb, are borne on the terminal joint.

The second antenna consists of a two-jointed basal portion or protopodite which carries two rami, one of which (fig. 25 *ex*), is obscurely divided into three nearly equal joints, while the other (fig. 25, *en*), is divided into eight very distinctly marked joints. Both at this stage and later the appendage possesses considerable power of rotation, and sometimes the branch *ex*, and sometimes the branch *en*, is on the outer surface. It is therefore very difficult to decide from an examination of this appendage alone which branch is the exopodite and which the endopodite ; but, as I shall show further on, a comparison with other appendages at a later stage indicates that the eight-jointed ramus is the endopodite, although the limb is frequently, and perhaps generally, carried in a position which brings this branch on to the outside. At this stage the locomotor hairs of both branches are confined to the tips of the terminal joints. The first and second joints of the endopodite are quite short, while the other six are longer and nearly equal in length.

The mandible consists of a short unjointed basal segment, which carries a one-jointed endopodite, and an obscurely three-jointed exopodite. Each branch carries three hairs, which are somewhat longer than the limb, and the entire length of the appendage, including the hairs, is about equal to the length of the first or second

antenna, without its hairs. There are no cutting blades or hooks upon the basal joints of either pair of antennæ or the mandibles.

The labrum (*L*) is somewhat larger and more prominent than it was at the stage before, and the anus is still absent.

### *The second free* Nauplius *stage or meta*-Nauplius.

In about twelve or fourteen hours the *Nauplius* sheds its skin and assumes the form shown in Plate 3, fig. 26. From the prominence of the region of the hind body, and the presence of a carapace, CLAUS has distinguished this stage of development, in allied forms, by the name of meta-*Nauplius*.

I did not actually witness the change, and am not sure of the exact length of the first free *Nauplius* stage, but it is not more than eighteen, and probably no more than twelve hours long. A *Nauplius* which had hatched from the egg some time during the latter part of Monday night was placed, alone, in a watch-glass of sea-water, and changed into the one from which fig. 26 was drawn before 9 P.M. on Tuesday evening.

The differences between this and the preceding stage are sufficiently great to attract the attention at first sight. The length, as measured from the ocellus to the posterior end of the body, has increased from $\frac{8}{1000}$ inch to $\frac{9}{1000}$ inch. The labrum (*L*) is longer and more prominent. The first antennæ (*A*) are unjointed, and the joints of the second antennæ (*An*) and mandibles (*M*) are almost absent.

The hairs at the tips of the endopodites of the second antennæ and mandibles (*en*) are irregularly plumose, and a long slender slightly curved hair is carried by each of the larger joints of the endopodite of the second antennæ.

On the inner posterior edge of the basal joint of the mandible, a short stout curved hook or blade has made its appearance. The four pairs of buds on the ventral surface, posterior to the labrum, are in the same condition as before, but the telson (*T*) is quite prominent, notched or forked, and furnished with two pairs of short stout spines, the inner pair being much longer than the outer. A well-marked fold (*c*) of the surface of the body now marks the posterior and the lateral edges of the carapace, but this line is not continued on to the anterior end of the body, and the posterior edge is not yet raised or separated from the hind body as it is, according to METSCHINCKOFF, in the last *Nauplius* stage of *Euphausia*.

The pigment-spots (*p*) are drawn out in such a way as to surround a large rectangular area, at the posterior end of the carapace, and in the region where the heart is placed at the next stage.

The digestive tract is now visible in a side view. The œsophagus (*œ*) runs upwards and forwards from the mouth, situated under the overhanging tip of the labrum, and then bends backwards and upwards to open into the floor of the stomach (*s*) ; the side walls and top of the stomach could be made out without difficulty, but I was not able to decide whether its ventral wall is complete or not. It is divided by a fold or flap

in its dorsal wall into a small rounded anterior chamber, into which the œsophagus opens, and a longer posterior chamber, with its dorsal wall very thick, which gives rise at its posterior end to the intestine (*i*). The greater part of the anterior chamber lies in front of the œsophageal opening. On each side of the stomach there is a group of polygonal yolk-cells (*l*), which are by no means as conspicuous as they were at an earlier stage. The intestine is small, with thin walls, and it follows the dorsal curvature of the body to the anus, which was visible in a ventral view just in front of the spines of the telson, at the point marked (*a*) in fig. 26. The cerebral ganglia (*ga*), and the ocellus (*oc*), are still visible, and underneath the stomach there is an elongated granular body (*n*), obscurely divided into segments, which is, without doubt, the rudimentary ventral nervous system.

As it was necessary to keep this larva alive I did not dare to use much pressure whilst examining it, and was therefore unable to make a very thorough study of its internal structure.

### *The first* Protozoëa *stage.*

On Tuesday evening, September 28th, at 9.30 P.M., the *Nauplius* which has just been described was placed alone in a watch-glass of sea-water, and at 9 A.M. on Wednesday, the 29th, it had changed into the larva which is shown in dorsal view in Plate 3, fig. 27. The number of segments and appendages of this larva and its general form and proportions are like those of the *Euphausia*, *Penæus*, and *Sergestes* larvæ at the stage of development which CLAUS has proposed to call a *Protozoëa* ('Crustacean System,' p. 2). The precise time when the change took place could not be learned, but there is reason to believe that it was not much later than the middle of the night. On September 14th I obtained, by dipping with a surface-net, a *Protozoëa*, which I studied and drew. It was of exactly the same size ($\frac{20}{1000}$ of an inch measured from the tip of the rostrum to the bases of the spines of the telson) as the one which moulted from the *Nauplius*, and it agreed with this in every respect except that the free segments of the hind body, shown in fig. 27, were wanting. It hardly seems probable that there are two stages of exactly the same size between 9.30 P.M. and 9 A.M., and it is much more probable that the body segments do not become distinct until some time after the moult, and as the larva had them at 9 A.M., I infer that it was nearer the end than the beginning of the first *Protozoëa* stage, and that the change had taken place some hours before I examined it.

CLAUS is inclined to believe that the difference between FRITZ MÜLLER'S last figure of the *Nauplius* of *Penæus* and his first figure of the *Protozoëa* is so great that there must be a gap in the series of observations. The isolated *Nauplius* of *Lucifer* passes through quite as great a change in twelve hours, and its length increases from $\frac{9}{1000}$ to $\frac{20}{1000}$, or more than 100 per cent., and there does not seem to be any necessity for supposing that FRITZ MÜLLER has missed a stage in order to account for the change in his larva.

In the case of *Lucifer* the actual increase in size is not very great, but the carapace becomes folded out over the body, and the thick posterior portion of the body of the *Nauplius* becomes pulled out into the long free movable hind body of the *Protozoëa*, so that the length is more than doubled, while the vertical thickness of the body is correspondingly reduced. The shape of the larva when seen from one side will be understood by a reference to Plate 4, fig. 35, for although this figure was drawn from an older larva, it correctly represents a side view of fig. 27 in all essentials.

The most marked differences between the meta-*Nauplius* of *Lucifer* and the *Protozoëa* are due to the development of the carapace and the hind body. The carapace (fig. 27) is horse-shoe shaped, with smooth lateral and posterior edges, and it forms about one-half of the total length of the body. On the median line of the anterior edge it is drawn out into a long rostrum (*R*), at the base of which are the cerebral ganglia (*ga*) and the ocellus (*Oc*). On the median line of the posterior edge of the dorsal surface there is a shorter dorsal spine (*ds*), and at the outer angles of the posterior edge a pair of lateral spines (*ls*), which are a little longer than the dorsal one. The side view (fig. 35) shows that the sides of the carapace have folded down on to the sides of the body, and all the appendages, except the antennæ, are almost completely covered by it. The appendages are so nearly alike in this and the next stage that it will be most convenient to describe them together.

The stomach (*s*) is now divided into a pair of anterior or cephalic, and a pair of posterior or hepatic lobes, and between the cephalic lobes a number of muscular fibres run upwards and forwards from the œsophagus to be attached (at *m*) to the carapace. The intestine is small and straight (*i*), but it is not of uniform character, and is divided into a series of small enlargements separated from each other by constricted portions.

The last of these enlargements is much more constant than the others, and its walls are attached to the integument of the abdomen by a number of small muscles.

It exhibits regular pulsations, which seem to draw water into and out of the anus (*a*), which is on the ventral surface of the telson.

The heart (*h*) is compact, short, situated near the posterior edge of the carapace, and it gives rise to a single median and two lateral anterior arteries.

The hind body is about as long as the carapace, and it is divided into four somites and a long unsegmented region (*abd*). The study of the appendages shows that the four somites are those which carry the third pair of maxillipeds (*Mp.* 3), and the first, second, and third thoracic somites (*T* 1, *T* 2, and *T* 3). There are no traces of appendages on any of them. The end of the unsegmented region of the hind body forms a well-marked flattened telson (*T*), which is slightly notched on the median line, and carries four pairs of stout spines, and one pair of very small ones. The small ones are nearest the median line ; the third pair are the longest and largest, and the fifth pair spring from the edges of the telson, some distance from the end.

*The second* Protozoëa *stage.*

As my season's work at the sea-shore ended the day the *Nauplius* shown in fig. 26 turned into the *Protozoëa* shown in fig. 27, I was not able to trace the development of that specimen; but on September 14th I had captured and drawn a larva in the same stage, and this moulted, while isolated in a watch-glass, into the second *Protozoëa* which is shown from above in Plate 3, fig. 34, and from the right side in Plate 4, fig. 35.

This larva measures $\frac{27}{1000}$ inch from the tip of the rostrum to the fork of the telson. The appendages are like those of the first *Zoëa* in number and structure, but there is a well-marked difference in the shape of the body. The carapace is somewhat elongated, its anterior edge is less perfectly rounded than before, and a pigment-spot (fig. 34, *E*) represents the future compound eye.

The pouches of the stomach (*s*) are much more conspicuous than before, and the œsophagus (fig. 34, *œ*) is visible in a dorsal view, between its anterior or cephalic lobes. The four somites of the hind body (*Mp.* 3, *T* 1, *T* 2, and *T* 3) have become short, but there is, as yet, no trace of their appendages. The unsegmented portion of the abdomen (*abd*) has increased in length, as have also the spines of the telson (*T*). The two pairs of antennæ have substantially the same form that they had during the *Nauplius* stage, and they are still the chief locomotor organs. The larva swims by jerks like a *Nauplius* or a Copepod.

The appendages at this as well as at the preceding stage are as follows (see Plate 4, fig. 35): the long uniramous first antennæ (*A*); the biramous second antennæ (*An.*); the cutting mandibles (*M*); the biramous first and second maxillæ (*Mx.* 1, *Mx.* 2); and two pairs of biramous maxillipeds (*Mp.* 1, *Mp.* 2).

The first antennæ consist at both stages (figs. 27, 34, and 35, *A*) of a long cylindrical basal joint which carries a few short hairs, and a short pointed terminal joint or flagellum, which ends in two long rather thick sensory hairs.

The second antennæ (figs. 27, 34, and 35, *An*; and fig. 36) are the chief locomotor organs, and are made up of a short stout two-jointed basal portion, a longer unjointed exopodite (*ex*), with four long terminal swimming hairs, and a longer endopodite (*en*), which is made up of two short proximal rings, and a series of six longer joints, each of which carries one, and the terminal one four, long slender swimming hairs.

Underneath the rostrum (fig. 35, *R*) there is a little elevation upon which the ocellus (*Oc*) is situated.

The labrum (fig. 35, *L*) has been carried on to the ventral surface of the body, and its anterior angle has become produced into a short stout, sharp spine, which is extremely small during the first *Protozoëa* stage.

As has been stated, the compound eye is represented at the second stage by a pigment-spot (fig. 35, *E*).

The mandibles (*M*), (figs. 27, 34, 35), have become reduced to cutting blades, which are visible in a dorsal view, and all traces of the *Nauplius* limb have disappeared.

During the first *Protozoëa* stage (Plate 3, figs. 28 and 29) it has only one denticle, which is large and pointed, and situated at the posterior angle of the cutting edge; but at the second *Protozoëa* stage (Plate 4, fig. 37) a number of smaller denticles have appeared in front of the long one. The mandibles are never quite symmetrical, but the outline of the left always differs a little from that of the right.

The external surface of the first maxilla of the first *Protozoëa* is shown in fig. 30, and the posterior surface of that of the second *Protozoëa* in Plate 4, fig. 38. It consists, at both stages, of a basal portion made up of two joints with cutting hairs (fig. 38, 1 and 2); a two-jointed endopodite (*en*), with three long slender hairs; and an exopodite or scaphognathite (figs. 30 and 38 *sc*), with three long slender hairs. In the first stage (fig. 30) the hairs of the scaphognathite are simple, but in the second stage (fig. 38) they are plumose.

The posterior surface of the second maxilla of the first *Protozoëa* is shown in Plate 3, fig. 31, and that of the second *Protozoëa* in Plate 4, fig. 39. It consists of a many-jointed basal portion (*b*), a two-jointed endopodite (*en*), and a scaphognathite or exopodite (*sc*). The whole inner edge of the appendage carries short stout hairs; the tip of the endopodite a few somewhat longer hairs; and the scaphognathite three slender plumose hairs, which are much longer in the second than in the first stage.

The first maxilliped (figs. 32 and 40) is very similar to the second antenna, and consists of a two-jointed basal portion, a four-jointed endopodite, and an unjointed exopodite. The inner edge is set with short stout hairs, which are simple in the first, but irregularly plumose in the second *Protozoëa* stage. The terminal joint of the endopodite carries four long slender simple hairs, and the tip of the exopodite four long straight slender hairs, which are plain in the first but regularly plumose in the second stage.

The second maxilliped of the first *Protozoëa* is shown in fig. 33, and that of the second *Protozoëa* in fig. 41. It is essentially like the first maxilliped in structure, but much smaller, and apparently of little functional importance.

In the second stage there is a small convoluted shell gland (fig. 35, *sg*), which appears to open at the base of the first maxilla; but the constant and violent movements of the limbs render it difficult to decide with confidence exactly what its relation to them is, and it is possible that its opening is upon the base of the second instead of first maxilla.

In the second *Protozoëa* stage the two pigment-spots (*p*) on the carapace become extremely dendritic, and a pair of anal pigment-spots (Plate 3, fig. 34, *pp*) make their appearance on the telson on each side of the anus.

At this stage the area, when the œsophageal muscles are attached to the carapace, is somewhat peculiarly marked by six little circles arranged in a pentagon, as shown, highly magnified, in fig. 35*a*.

*The last* Protozoëa *stage* (Erichthina).

The change from the last stage to the next one in the series was actually observed in several specimens, and more than fifty larvæ passed through it in the laboratory.

After the moult the larva, which is shown from the ventral surface in Plate 4, fig. 42, and in outline in fig. 42*a*, has the characteristics of Dana's genus *Erichthina*.

Its length, from the tip of the rostrum to the end of the telson, has increased to about $\frac{27}{1000}$ inch, and most of the increase is in the hind body. The carapace also is somewhat elongated (it was a little flattened by pressure in the specimen which was drawn), and the outline of the anterior edge is no longer regularly curved. At the base of the rostrum there is a slight eminence where the integument is pushed out a little by the optic ganglion, and at the outer angle there is a much larger eminence which is the rudimentary cornea of the compound eye. The eye itself is now represented by a large conspicuous pigment-spot (fig. 42*a*, *E*).

The appendages have undergone extremely little change, and they are, as before, as follows: the first antennæ (*A*), the second antennæ (*An*), the mandibles (*M*), the two pairs of maxillæ (*Mx.* 1 and *Mx.* 2), and two pairs of maxillipeds (*Mp.* 1 and *Mp.* 2). The second antennæ are still the chief organs of locomotion.

The hind body is much longer than it was at the stage before, and it is now somewhat longer than the carapace. It now consists of nine free segments and an unsegmented portion (*A* 5, 6). The first of the free segments (fig. 42, *Mp.* 3) is much narrower than any of the others, and its outer edges are marked by enlargements which appear to be the rudimentary appendages, the third pair of maxillipeds. None of the segments which follow it show a trace of the appendages, and the thoracic and abdominal ganglia are not yet visible.

The four segments which follow next after the one with the bud-like processes have rounded posterior edges, while the posterior edges of the next four are pointed. The later history seems to show clearly that those with rounded edges are the first, second, third, and fourth thoracic somites, and that the following ones are the first, second, third, and fourth abdominal somites. It will be seen, then, by a comparison of this with the earlier and later stages, that the somites of the body are all developed in regular order, from in front backwards, but that the first abdominal somite follows immediately after the fourth thoracic, while the fifth thoracic is never developed. At this stage the long unsegmented region (*A* 5, 6), represents the fifth and sixth abdominal segments and the telson. The two anal pigment-spots are larger than they were during the stage before, and from this time to maturity their colour is a dirty reddish-brown instead of black.

*The* "Zoëa" *stage* (Elaphoearis *stage of* Sergestes.)

After the next moult, which was observed in a great number of specimens, the larva passes into a stage which is directly comparable, so far as the appendages are

concerned, with the *Elaphocaris* stage of *Sergestes*, although the most conspicuous features of the *Elaphocaris* larva, the long compound spines, are not present in *Lucifer*. It is now about $\frac{50}{1000}$ inch long, and it is shown in a dorsal view in Plate 5, fig. 44, and, more highly magnified, from below in Plate 4, fig. 43. In a side view (fig. 45) it still agrees pretty closely with fig. 35; its body is carried in the same attitude, and the antennæ are still the chief organs of locomotion. The fully-developed appendages are, as before, the first and second antennæ, the mandibles, two pairs of maxillæ, and the first and second pairs of maxillipeds, but the third pair of maxillipeds, four pairs of thoracic appendages, and the swimmerets or appendages of the sixth abdominal somite are now present as rudimentary buds.

The compound eye (figs. 43 and 45, *E*) is now well advanced in development, although there is as yet no trace of a stalk, and the cornea is simply a modified portion of the integument of the carapace.

The carapace is longer, narrower, and more rectangular in a dorsal view than it was at the last stage, and it makes only about one-third of the total length of the body of the larva. Its pigment-spots are very large, dendritic, and conspicuous, but their colour has changed from black to dark reddish-brown.

The anterior lobes of the stomach (fig. 44, *s*) have lengthened and approached each other on the median line, and they now reach forwards nearly to the optic ganglia.

The appendages which were present during the *Protozoëa* stage have essentially the same structure now, and the differences are very slight. The number of cutting hairs on the basal joints of the first maxilla (fig. 46) has increased; the hairs on its endopodite are plumose, and one of those carried by the scaphognathite is much longer than the other two. This is the case also with the second maxilla (fig. 47), and the hairs along its inner edge have become almost as long and slender as those at its tip. The first maxilliped (fig. 48) is almost exactly like that of the *Protozoëa;* but the second (fig. 49) is much more developed, and the hairs on its exopodite are plumose.

The hind body is now divided into its full number of segments; that of the third pair of maxillipeds (*Mp.* 3); the first, second, third, and fourth thoracic somites (*T* 1, *T* 2, *T* 3, and *T* 4); and the six abdominal somites, but the telson (*T*) is not yet completely distinct from the last abdominal somite. The thoracic somites are shortened and crowded together, and each of them carries a pair of bilobed buds, the rudimentary thoracic appendages. These buds are crowded together in a double row on the median line of the ventral surface of the body, and outside them is a pair of much larger buds (figs. 43 and 45, *Mp.* 3), bilobed also, but pointing backwards; the rudimentary third pair of maxillipeds.

The future history of the larva seems to show conclusively that the inner set of buds are, as indicated in fig. 43, the first four pairs of thoracic limbs or pereiopods. The side view (Plate 5, fig. 45) shows that there is no other pair in front of or

behind them, and the fifth thoracic somite is entirely wanting, nor are its appendages present at any stage in the development of *Lucifer*.

The abdomen is much longer than it was at the last stage, and all its segments (fig. 43, *A* 1, *A* 6) are present, although the last one (*A* 6) and the telson (*T*) are not yet entirely separated.

The ventral surface of the sixth abdominal somite is armed with a pair of long stout spines over the base of the swimmeret, or sixth abdominal appendage, which is shown in fig. 43 as a long, bilobed pouch or bud, which reaches nearly to the tip of the telson. The third, fourth, and fifth abdominal somites carry, close to the anterior edge of the ventral surface, irregular groups of reddish-brown pigment-spots, which do not seem to be present in all specimens. The thoracic spots (fig. 44) and the anal spots (fig. 45) are usually a little more red than before, but they are nearly black in some specimens. The abdominal ganglia, which could not be distinctly made out in the last *Protozoëa*, are now very conspicuous, as shown in the ventral view (fig. 43). They lie near the posterior edges of the somites, and their halves are united in the median line, although the commissures between the ganglia are quite widely separated.

The spines on the telson have lengthened, but their number, arrangement, and relative size is the same as before. Their proximal ends from the base about half-way to the tip are marked by fine serrations, which appear to be short hairs, which have not been perfectly extended.

### *Schizopod or* Sceletina *stage* (Acanthosoma *of* Sergestes).

Up to this time the mode of locomotion has been by means of short, jerking *Nauplius* leaps, and the two pairs of antennæ have been, as they were when the larva left the egg, the chief organs of locomotion. The structure of these appendages has remained extremely constant through all the moults, but they now change their character entirely, and lose their locomotor function.

The change which is undergone by the larva at the end of the *Zoëa* series is very much greater than it has been at any preceding moult, except that between the *Nauplius* and the first *Protozoëa*, and in some respects it is even greater than it was at that time. After the moult it is a Schizopod (Plate 6, fig. 50), about $\frac{70}{1000}$ inch long, with seven pairs of long jointed biramous swimming feet, fringed with long slender hairs. The swimmerets are also present as functional appendages, with long fringing hairs.

This stage differs from those which have gone before in this, that it persists with slight change for several moults, while there has been considerable change at each of the preceding moults. It is shown from below in fig. 50, as it appears immediately after the moult which follows the stage shown in fig. 43.

The figure was drawn from a *Zoëa* which was captured at the surface of the ocean,

carefully examined and compared with fig. 43, and found to agree with it exactly. It was then placed alone in a small beaker of sea-water. The next day it was found to be moulting, and the drawing (fig. 50) was made from it immediately after the completion of the moult. Other specimens, like fig. 50, were kept until they changed their skins, and assumed a form a little larger than fig. 50, but similar to it in all respects except that the abdominal appendages were now present as small buds. Some of these were kept until they changed into larvæ like the one which is shown, less highly magnified, from the side, in fig. 54. The abdominal appendages were now quite long, but still rudimentary, and the general form of the larva from above or below, as well as the form, number, and arrangement of the thoracic appendages and mouth parts, was like fig. 50.

When seen from above or below (fig. 50) the carapace has nearly the same shape that it had during the *Zoëa* stages, but it now makes less than one-third of the total length of the body, and a side view (fig. 54) shows that it is now only a little deeper than the body, so that the basal joints of the thoracic limbs and maxillipeds are exposed below its inferior border. The posterior dorsal spine and the two postero-lateral spines have disappeared, and a pair of long antero-lateral spines (fig. 54, *s*), nearly half as long as the rostrum, have made their appearance underneath the eyes. The rostrum (fig. 50, *R*) has the same shape and about the same relative length as before, and the ocellus (*Oc*) is still present at its base.

The compound eye (*E*) is mounted upon a movable stalk, which is quite short during the first Schizopod stage, but it soon lengthens, as shown in fig. 55, which is a dorsal view of the anterior end of the carapace of the larvæ shown in fig. 54.

The first antenna has undergone more change at this than at all the previous moults together. It is now about as long as the carapace, and each of the two long cylindrical joints (fig. 50), which make up its basal portion, carries on its inner edge three long slender two-jointed delicately plumose hairs. The base of the proximal joint is swollen and carries a small hook-like process on its inner edge. The two long sensory hairs have disappeared from the tip, which is unsegmented, pointed, and ends in a bunch of short hairs. This appendage changes slightly with each moult, and in the third Schizopod stage (fig. 54) the distal half of the proximal joint (fig. 56) has separated from the proximal joint, so that the shaft is made up of three instead of two portions. The hook is still present on the swollen base of the first joint, and behind it the otocyst (*e*) has made its appearance. The terminal joint or flagellum has now lengthened, and it carries three long sensory hairs which spring from about the middle of its outer surface.

The changes which the second pair of antennæ undergo at this moult are even greater than those which take place in the first pair. Their locomotor function is lost; the long swimming hairs have disappeared; and in the first Schizopod stage (fig. 50) the appendage is quite rudimentary, unjointed, less than one-half as long as the first antenna, and divided into an exopodite and an endopodite which are nearly

equal in length, although even at this stage the endopodite is a little the longest. Each ramus ends with a pair of very short hairs.

The appendage now changes with each moult, and in the third Schizopod stage (fig. 54) the exopodite has become a scale (fig. 57, *ex*) while the endopodite (*en*) has elongated, and now forms a seven-jointed flagellum, about as long as the first antennæ or the carapace. The basal joint (fig. 57, *b*) is thick and swollen, the two proximal joints of the flagellum (2 and 3) are short; the next (4) long, and the other four about equal in length, and about half as long as the joint (4).

Through all the Schizopod stages the structure of the labrum (*L*) is about as it was in the *Protozoëa* and *Zoëa*, and its interior angle is still produced into a short stout sharp spine.

The mandibles are cutting jaws with no trace of a palpus, and at the first Schizopod stage (fig. 51) the denticles are numerous and of nearly uniform size. In the last Schizopod stage (fig. 58) a second set of denticles has appeared on the outer surface of the blade a short distance from the cutting edge.

The first maxilla (fig. 52) is very much like that of the *Protozoëa* and *Zoëa*, but the cutting hairs upon the two basal joints (1 and 2) are more numerous, and a small slender plumose hair has appeared near the edge of each joint. The scaphognathite is small and has only two hairs, which are less regularly plumose than before.

The scaphognathite of the second maxilla (fig. 53, *sc*) is now rudimentary and has no hairs. The hairs on the inner edge of the appendage are shorter than they were during the *Zoëa* stage, and all of them are plumose and about equal in length.

The first maxilliped (fig. 50, *Mp.* 1) has not changed very much, although its joints are nearly absent. The exopodite is about as long as the endopodite, and all the hairs on the appendage are short and plumose.

The second and third maxillipeds and the four pairs of thoracic appendages are well developed, as a series of long biramous or Schizopod feet, which are essentially alike in form and structure, and, with the telson and swimmerets, now form the locomotor apparatus of the larva, which no longer swims by jerks but darts through the water with great rapidity, and is able to offer considerable resistance to the suction of a dipping tube. Each swimming foot consists of a two-jointed basal portion or protopodite, a long four-jointed endopodite, and a much shorter exopodite. The exopodite is flat, pointed, and its outer or distal half is marked by a series of six pairs of notches, or annulations, close together. The terminal joint carries a pair of long slender unplumose hairs, and a pair of similar hairs springs from each annulation, so that there are fourteen hairs in all on each exopodite, arranged so as to form a large fan-shaped paddle at the tip of the limb. The terminal joint of the endopodite is much shorter than the others, and it carries six long plumose hairs. The first appendage in this series, the second maxilliped (fig. 59, *Mp.* 2), is somewhat rudimentary: the endopodite is scarcely longer than the exopodite, and its hairs are short. The next or third

maxilliped (*Mp.* 3) is more like those which follow, but its hairs are shorter. The first, second, and third pereiopods are about equal in length, and they have the typical structure which has just been described; but the endopodite of the fourth (*Pr.* 4), like that of the second maxilliped, is shorter than the exopodite, although its hairs are very long.

At the last Schizopod stage (fig. 54) the series of limbs, shown from above in fig. 59, is about as it is in the first stage, but the hairs on the endopodites of all the appendages, except the last, are short. A comparison of one of these appendages with the second antenna of the *Nauplius* or *Protozoëa* or *Zoëa* shows great similarity, and I am therefore disposed to believe that the long jointed ramus of the antenna is homologous with the long ramus of the thoracic limb, and consequently the endopodite.

The abdomen is very much longer in proportion to the carapace than it was at the "*Zoëa*" stage, and a comparison of figs. 50 and 54 with fig. 43 will show that it has become flattened from side to side, while its vertical thickness has greatly increased. All six somites are distinct, but at the first Schizopod stage there are no traces of any abdominal feet except the swimmerets, which are large and perfect. In the second Schizopod stage the first five pairs of pleopods are represented by short buds, and in the last Schizopod stage (fig. 54) they have nearly or quite their full size, but are still rudimentary.

The posterior edge of the ventral surface of each abdominal somite carries a couple of spines (fig. 50) pointing backwards. They are small on all the somites except the last, and they appear to correspond to those which, from their great size, have given the name *Acanthosoma* to the larva of *Sergestes* at the same stage of development. The sixth abdominal somite also has a small median dorsal spine.

The telson (*T*) is movable, greatly elongated, three times as long as wide, and its spines have become very small, although in number, arrangement, and relative size they agree with those of the *Zoëa* and *Protozoëa*.

The sixth pleopod or swimmeret consists of a short thick basal joint, a long flat exopodite which is serrated along its inner edge and free extremity, but smooth along its outer edge; and a flat endopodite serrated on both sides. Each serration carries a long slightly curved plumose hair, and the outer edge of the exopodite has a small tooth at its outer end. From the base to the tooth the outer border is nearly straight and parallel to the inner border, but the end of the appendage is prolonged into a rounded tip which reaches beyond the tooth. In the first Schizopod stage there are eight hairs on the inner border and four on the end of the exopodite, or twelve in all; and there are eight hairs on the endopodites, but the number of serrations and hairs increases rapidly with each moult, on each division of the limb, and they are much more numerous in the last Schizopod stage, as shown in fig. 54.

A large reddish-brown pigment-spot (fig. 54, *p*) has now appeared on each side of

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the fourth abdominal segment, and the anal spots are large, with a dull red tinge. The spots on the carapace disappear at the end of the *Zoëa* series.

### *The* Mastigopus *stage.*

After the next moult the larva (Plate 7, fig. 60) assumes a form which is essentially like that of the adult, but with numerous slight differences, the most important of which are the shortness of the flagellum of the first antenna and the absence of the neck or elongation of the carapace. In these respects, as well as in the number, character, and relative size of the appendages, it now agrees very closely with the young *Sergestes* or *Mastigopus*.

The size of the thorax is reduced, while the abdomen has grown larger and longer. The exopodites of the maxillipeds and first three pairs of pereiopods have disappeared, together with every trace of the fourth pereiopod. The abdominal appendages are perfect; the first is made up of an elongated basal joint, which carries a single terminal branch of about the same length as the basal joint, but pointed and fringed with long slender swimming hairs. The four appendages which follow are each furnished with two terminal branches instead of one, but are similar in other respects. The larva now sheds its skin several times, and grows with each moult; but the process of change into the adult is, with the exception of the elongation to form the neck, simply a process of growth, as the appendages and somites all have essentially their adult character.

A larva about one-fifth of an inch long, two moults after the last Schizopod stage, is shown from the side, magnified about fifty diameters, in Plate 7, fig. 60. The first antenna (*A*) is a little more than twice as long as the eye-stalk, and consists of a stout three-jointed basal portion, which forms about two-thirds of the total length of the appendage, and a short, thin, two-jointed flagellum. The scale (*ex*) of the second antenna is only a little longer than the eye, while the flagellum (*en*) is more than half as long as the body of the animal, measured from rostrum to telson, and is made up of thirteen small joints and two thicker basal joints.

The carapace has elongated considerably, and the neck (*n*) makes nearly half its length. The anterior end of the carapace has a dorsal rostrum (*R*), two much shorter lateral spines (*ls*), and a very small spine on each side close to the anterior edge and about half way between the rostrum and the lateral spine. The cephalic lobes of the stomach extend into the neck, and reach nearly to the basis of the eye-stalks. The coiled antennal gland (*g*) has made its appearance. The carapace proper (*c*) has a pair of anterior spines, but none on its posterior margin. The labrum (*L*) has a much greater relative size than it had during the Schizopod stages, but its spine disappears at the end of the last Schizopod stage. The mouth parts and thoracic limbs have their adult character, and will be noticed at length in the description of the adult. A reddish-brown pigment-spot has now appeared between the bases of the eye-stalks;

another at the base of the telson; and the dorsal surfaces of the fifth, fourth, and sometimes the third abdominal somites are irregularly marked, near their posterior edges, by patches of the same colour. The anal pigment-spots are of a dirty red colour.

### *The* Lucifer *stage.*

The specimen from which fig. 61 was drawn was a little more than half an inch long, or about half as large as an adult specimen. It differs in several particulars, besides size, from an adult male, but in all respects except size and the presence of reproductive organs it is exactly like a mature female. Its appendages are like those which are shown in figs. 63 to 70, although these were drawn from an adult female specimen.

The adult structure of our American species has been described by Faxon ('Studies from the Biological Laboratory of the Johns Hopkins University,' vol. i., part iii.); but as he had only a single male specimen, which had been preserved in alcohol, his account was necessarily somewhat incomplete.

The first antenna (Plate 7, fig. 61, and Plate 8, fig. 66, *A*) is about as long as the carapace and neck, and it is divided into two nearly equal portions, the base (fig. 66, 1) and the flagellum (fig. 66, 2). The base is divided into three joints, the first about as long or a little longer than the eye, the second much shorter, and the third still shorter. The large ear occupies the centre of the proximal end of the first joint. On the outer end of the first joint and on the second there is a row of six short, equal, plumose hairs, three on each joint. The flagellum is made up of ten joints; the first and second are thicker than the others, and the first carries two and the second three sensory hairs. The terminal joint of the flagellum is much longer than the other, and carries a few very short hairs at its tip.

The second antenna (figs. 61 and 66, *An*) is, in the fully-grown specimen, almost twice as long as the first, and nearly or quite as long as the body. It consists of a very short basal joint (fig. 66, 3), which carries the scale (*ex*) and the flagellum (*en*). The scale is somewhat longer than the eye, flat and narrow, and its inner edge carries nine and its tip three long, slender, plumose hairs, which are about half as long as the scale itself. The flagellum tapers gradually from the base to the tip, and is made up of twenty-four joints, each of which carries a pair of very short hairs. The joints at the tip of the flagellum are a little longer than those at the base. The living animal usually carries these appendages extended before it, and diverging a little at their tips. It occasionally throws them back along the sides of the body, but only for an instant at a time.

The eye-stalk tapers gradually from the base to the tip, and there is no abrupt distinction between the stalk and the eye proper, as there appears to be in other species. The length of the eye, with its stalk, is a little less than that of the true carapace.

The neck makes a little more than three-fifths of the total length of the carapace,

and its vertical diameter is more than half that of the thorax. It has a median dorsal rostrum (fig. 61, *R*), which is much smaller relatively in the adult than in the young, and two antero-lateral spines (*ls*). About half-way between the rostrum and the lateral spine the anterior edge of the neck has an extremely minute spine on each side, as in the younger stage last described. The cerebral ganglia (*cg*) occupy the ventral half of the anterior end of the neck, and the long commissures can be seen at *co.* running back to join the ventral nervous system. The cephalic lobes of the stomach (*s*) and the antennary gland (*g*) occupy the dorsal portion of the neck.

The true carapace (*c*) does not reach down on to the sides of the body as far as the basal joints of the thoracic limbs and mouth parts, and both these and their ganglia (figs. 75 and 76, *tg*) are visible below its free edge. Its edges are smooth, but there is a small spine at its anterior end.

The labrum (fig. 61, *L*) is massive and prominent, but there is no trace of a spine.

The inner surface of the mandible (fig. 62) is marked by a number of parallel ridges, one for each denticle; and there is a second, and a faint trace of a third, series of denticles on the outer surface (fig. 63). There is no trace of a mandibular palpus.

The scaphognathite of the first maxilla (fig. 64) has disappeared, the endopodite is rudimentary, while the second basal joint is very much larger than the first, and carries about fifteen stout short hairs arranged in three rows. The first joint has four much larger unequal hairs, which are serrated. The outer edge of the first and both edges of the second joint carry a single delicate plumose hair each. Fig. 65 shows the inner surface of the second basal joint.

The second maxilla (Plate 8, fig. 67) is more like that of the larva. There is a three-jointed inner portion with short stiff hairs, and an extremely large scaphognathite (fig. 67, *sc*), which is long and narrow, and united to the body of the appendage by a very narrow stalk. The outer end carries three rather stiff, short, plumose hairs, and five similar but somewhat longer hairs arise from the inner surface between the outer end and the area of attachment. The inner end carries four plumose hairs, three of which are almost as long as the scaphognathite itself, while the fourth appeared to be broken off in the four specimens which I dissected out.

The first maxilliped is a short, stout, two-jointed appendage (Plate 8, fig. 68), convex on its outer but flat on its inner surface, and fringed with short, stout, plumose hairs.

The second maxilliped (Plate 7, fig. 61, *Mp.* 2, and Plate 8, fig. 70) is a long jointed limb, bent into a knee, and formed of six joints. It is fringed by long plumose hairs, which, on all the joints except the first and second, are arranged in a single row. The first and shortest joint has no hairs; the next, or second, has one row of five and one row of three; the next, or third, has six hairs; the next, or fourth, and the fifth have ten each; and the terminal joint has six.

The next or third maxilliped (fig. 61, *Mp.* 3) is a long, slender, six-jointed limb, with a double row of short hairs.

The first pereiopod (fig. 61, *Pr.* 1) is four-jointed, and shorter than the last maxilliped.

The second and third perciopods (*Pr.* 2 and *Pr.* 3) are nearly equal, and twice as long as the first; they are four-jointed, have a double row of small hairs along the anterior edge, and the last ends in a small curved hairy claw.

They exhibit no trace of gills or of endopodites, and there is no stump to indicate the position of the fourth pereiopod, which disappeared at the end of the Schizopod period.

The first abdominal appendage of immature specimens or of mature females (Plate 9, fig. 74, *Pl.* 1) is made up of a thick basal portion, which is unjointed in young specimens but two-jointed in mature ones, and a pointed annulated terminal portion which is fringed with swimming hairs. In the nearly grown but immature male (fig. 76) there is a little bud or projection (*a*) near the base of the anterior surface of the long basal joint. In the sexually mature male (fig. 75) this bud has become the clasping organ which has been described by Milne-Edwards, Dana, Semper, Dohrn, Claus, Faxon, and others; and another smaller process or tooth has appeared upon the distal one of the two joints into which the base of the limb has now divided.

The second, third, fourth, and fifth pleopods consist, in the young of both sexes, and in the mature females, of a long unjointed basal portion and two hairy terminal branches. In the adult male the second pleopod has a third and smaller terminal branch, as Claus has pointed out (Zeit. f. Wiss. Zool., xiii., 434).

The first, second, third, fourth, and fifth abdominal somites end below in short spines, and they are all about equal in length, except the fifth which is nearly twice as long as any of the others. It has a median dorsal spine on its posterior edge, and the very young specimens also have a pair of postero-lateral spines, as shown in Plate 7, fig. 60. In older specimens this pair of spines disappears, as shown in Plate 9, fig. 72, and in the adult female the somite undergoes no further change. When the male reaches sexual maturity, however, the lower edge of the somite becomes produced, as described by Dana, on each side into the hooks shown in fig. 73. In our species the smaller one of these hooks is near the middle of the somite, and the larger one about half way between it and the posterior edge.

As shown in figures 72 and 73, the telson of an adult specimen is only about half as long as the swimmerets. The tip of the telson of an adult female is shown from above in fig. 71.

In the male the telson becomes somewhat bent (fig. 73, *T*) as maturity is reached, and a rounded anal papilla becomes developed in its lower surface, while the telson of the adult female remains like that of immature specimens of both sexes.

The exopodite of mature specimens usually has about twenty hairs, and the endopodite sixteen. The exopodite is longer and wider than the endopodite, and it is alike in both sexes until maturity is reached, when it becomes somewhat modified in the male,

This sexual difference has been pointed out by Dohrn (Zeit. Zool., xxi., 1871, p. 358), but it seems to have escaped the notice of all other observers.

In the young and in the mature female (fig. 72) the rounded tip projects beyond the tooth (*a*), but as the male approaches maturity the outer edge lengthens, thus pushing the tooth out, as shown in fig. 73, until the end of the appendage becomes square instead of rounded. It is extremely interesting to notice that in *Lucifer*, as in so many other animals, the adult female is infantile in all the secondary points of difference from the male.

### *General view of the metamorphosis of* Lucifer.

A review of the facts which have been described in this section indicates that some of the changes are much more significant than others, since the number of moults is much greater than the number of distinct larval type.

The meta-*Nauplius* is obviously a *Nauplius* with the rudiments of structures which are to appear after the moult, and it must therefore be regarded as a *Nauplius* prepared for the change into a *Protozoëa*, rather than a distinct stage of development.

There is no such break between the first *Protozoëa* and the last *Zoëa* as there is between the first *Protozoëa* and the *Nauplius*. The rudimentary pereiopods and swimmerets of the so-called *Zoëa* are nothing but a preparation for the next stage of development, and the supposed necessity for finding a stage which can be directly compared with the *Zoëa* of the higher Decapods does not justify us in making two larval types out of the unbroken series of *Protozoëa* and *Zoëa* forms.

It is obvious that the three Schizopod stages are modifications of a single larval type, and the presence of rudimentary pleopods in the second and third stages must be regarded as a preparation for the next stage of development.

There is no abrupt break between the so-called *Mastigopus* and the young *Lucifer* when it is a little older and the neck has appeared.

On the other hand, there is a real break between the *Nauplius* and the *Protozoëa*, and the change from one to the other is accompanied by profound structural changes. This is the case also with the transition from the *Zoëa* to the Schizopod stage ; and with that from the Schizopod stage to the young *Lucifer* stage. The same thing is true to a lesser degree of the change from the immature *Lucifer* to the adult male.

The metamorphosis may then be divided into the following well-marked stages, each of which except the last, and in all probability the last also, persists through more than one moult :—

1. A *Nauplius* stage.
2. A *Protozoëa* stage.
3. A Schizopod stage.
4. An immature *Lucifer* stage, which persists in the female.
5. An adult male stage.

If we neglect the features which, at the end of each stage, make their appearance as preparation for the next, we may describe each stage as follows :—

The *Nauplius* has three pairs of locomotor appendages, the first antennæ, the second antennæ, and the mandibles; and there is a large labrum without a spine, and the carapace and telson are absent. There is an ocellus, but no compound eyes.

The *Protozoëa* has two pairs of antennæ, which are like those of the *Nauplius*. The mandible is reduced to a cutting blade. There are two pairs of biramous maxillæ, with scaphognathites, and two pairs of biramous maxillipeds. There is a long hind body, ending in a flat telson. The labrum has a spine. The carapace is large, and has a rostrum, a median dorsal and two lateral posterior spines; and its free edges reach down beyond the basal joints of the appendages. There is an ocellus, but no stalked eyes.

The Schizopod stage is characterized by the great change in the two pairs of antennæ, which are no longer like those of the *Nauplius*, but have the characteristics of those of the adult. All the mouth parts and four pairs of thoracic limbs are present, and all posterior to the first pair of maxillipeds are biramous and locomotor. The abdomen has six somites and a movable telson. The swimmerets are present, but the other abdominal appendages are not.

The ocellus persists, but the stalked eyes are also present. The carapace has a rostrum and two antero-lateral spines, but those at the posterior edge have disappeared. The edges of the carapace do not reach over the basal joints of the thoracic limbs, and the body is flattened vertically. The labrum still has a spine.

The young *Lucifer* and the adult female have a long flagellum on the first antenna, a flagellum and scale on the second; the ear and antennary gland are present; the neck is elongated. The fourth pereiopod has disappeared, and the others, as well as the maxillipeds, have lost their exopodites. The first pleopod has one terminal branch, the next four two branches each; the sixth abdominal somite has a smooth lower edge. The telson is straight and the outer end of the exopodite of the swimmeret is rounded.

The adult male has a clasping organ on the first pereiopod, three rami on the second, two teeth on the lower edge of the sixth abdominal somite, a square end to the exopodite of the swimmeret, and a bent telson.

It is true that these five stages merge into each other somewhat, and that they are complicated by the presence of the rudiments of organs which are be functional at the next stage; but after all these secondary modifications are allowed for, it will be seen that each stage is sharply and definitely marked, and separated by a pronounced gap from the stages before and after.

The significance of these five stages can be best inquired into after the corresponding stages of other *Sergestidæ* have been examined, and I will return to the subject further on, in a section on the general relationships of the group.

## IV. History of the Appendages of Lucifer.

For convenience of reference I will now describe the changes which each appendage undergoes at each stage of development, going over the same ground once more, but in a different way.

### *The first antenna.*

In the egg *Nauplius* (figs. 21, 23, and 24, *A*) this appendage is unjointed, more than half as long as the body, and it carries a terminal tuft of hairs.

In the first free *Nauplius* (fig. 25, *A*) it consists of five nearly equal joints; it is nearly as long as the body of the second antenna, and its tip carries two long simple hairs and two much smaller hairs.

In the last *Nauplius* stage, or meta-*Nauplius* (fig. 26) the joints have disappeared; it is only about two-thirds as long as the body, and it carries only the two long hairs at the tip.

In the first *Protozoëa* stage (fig. 27, *A*) it is made up of a long cylindrical basal joint with a few short hairs, and a much shorter terminal joint, which is pointed, and carries the two long hairs as before.

The structure of the appendage does not change until the end of the *Zoëa* series, and it is shown at *A* in figs. 34, 42, 43, and 44.

At the first Schizopod stage (fig. 50, *A*) the basal portion is made up of one very long cylindrical joint, with a hook near its swollen base, and a much shorter distal joint. Three long, two-jointed, plumose hairs spring from the inner edge of the second joint, and three more from the inner edge of the distal third of the basal joint. The terminal portion has lost the two long hairs which it had at earlier stages.

In the last Schizopod stage (fig. 54, *A*, and fig. 56) the distal third of the basal joint has separated off as a distinct joint (fig. 56, 2) upon which the three hairs are situated. The ear has made its appearance, behind the hook, on the swollen base of the first joint. The terminal joint (4) carries three sensory hairs, which arise upon its outer surface about half way between its tip and base.

In the *Mastigopus* stage (fig. 60) the terminal joint has lengthened to form a two-jointed flagellum, and the appendage is more than twice as long as the eye.

In the young specimens which have attained to the adult form (fig. 61, *A*) the appendage is about as long as the carapace and neck, and in the adult (fig. 66, *A*) the flagellum (2) is about as long as the basal portion (1). It consists of ten joints, the terminal one longest, and the first and second thick. The first carries two and the second three sensory hairs.

The basal portion is thick, cylindrical, three-jointed, with six plumose hairs, and the ear nearly fills the enlarged base.

*The second antenna.*

In the egg *Nauplius* (fig. 24, *An*) this is unjointed, more than half as long as the body, divided into two nearly equal rami, with hairs at their tips.

In the first free *Nauplius* stage (fig. 25, *An*) a two-jointed basal portion carries a three-jointed exopodite and an eight-jointed endopodite. The appendage is nearly as long as the body, the two rami are about equal in length, and each has three long simple hairs at its tip. In the last *Nauplius* stage (fig. 26) the joints are obscure; the endopodite is longer than the exopodite; it has long hairs along its side, and those at the tip are plumose. In the *Protozoëa* stages (figs. 27, 34, 35, 42, 43, and 45, *An*, and fig. 36) it consists of a two-jointed basal portion (fig. 36), which carries an unjointed exopodite (*ex*) with long, slender, non-plumose terminal hairs, and an eight-jointed endopodite (*en*) with eight long hairs arranged along its side and tip. The first and second joints are very short, while the other six are longer and nearly equal.

In the first Schizopod stage (fig. 50, *An*) the appendage is rudimentary, its joints are absent, and the exopodite is almost but not quite as long as the endopodite. The appendage is only half as long as the first antenna. In the last Schizopod stage (fig. 54, *An*, and fig. 57) the exopodite has become a scale, which is only half as long as the seven-jointed flagellum which has become developed from the endopodite; the basal joint is simple, very large, and the appendage is as long as the first antenna.

The flagellum now grows rapidly, and in the adult (fig. 61, *An*, and fig. 66, *An*) it has twenty-four joints, and is more than half as long as the body. The antennal gland opens into its base, and the scale is longer than the eye, and carries twelve long plumose hairs.

*The mandible.*

In the egg *Nauplius* (fig. 24, *M*) this is biramous, unjointed, and tipped with hairs. In the first free *Nauplius* (fig. 25, *M*) it is short, and made up of a stout basal joint; a two-jointed exopodite with three long slender hairs, two of which are carried by the terminal and one by the proximal joint; and a shorter endopodite with three long simple hairs. In the last *Nauplius* stage (fig. 26, *M*) the joints of the exopodite have disappeared, the three hairs on the endopodite have lengthened and become plumose, and the inner edge of the basal joint carries a hook or blade. From the beginning of the *Protozoëa* series to maturity the mandible is a cutting blade, with no trace of a palpus, and the number of its denticles gradually increases with age.

*The metastoma.*

The manner in which the metastoma originates in the *Nauplius* as a pair of buds similar to those which become the maxillæ, as well as the fact that it persists in closely-allied forms as a pair of limb-like structures, seems to show, as Claus has

pointed out ('Untersuchungen,' &c., p. 15), that the Decapod metastoma is morphologically a pair of appendages; that it has been formed by the simplification and union of structures homologous with the limbs; and that this pair of appendages was originally furnished with a body-somite and a pair of ganglia. Claus's reason for the homology is the resemblance between the Decapod *Protozoëa* and the larva of Phyllopods and Copepods, and the manner in which these parts are developed in the Nauplii of *Lucifer* and *Euphausia* seems to be an additional reason for accepting his view.

*The first maxilla.*

This appendage is rudimentary during the *Nauplius* stages, but, as shown in fig. 21, *Mx.* 1, it is represented by a pair of buds several hours before birth.

In the *Protozoëa* and *Zoëa* series it has the form shown in fig. 46, which was drawn from the appendage of a larva in the last *Zoëa* stage. Its characteristics are developed gradually, and it is somewhat simpler during the earlier *Protozoëa* stages than it is in fig. 46. Fig. 30 shows it as it appears in the first *Protozoëa* when seen from the outside. It consists of a basal portion (fig. 46) made up of two joints (1 and 2), which carries a short obscurely-jointed endopodite (*en*) and a scaphognathite (*sc*). In my description of this and the other mouth parts of *Lucifer* I have accepted Claus's homology ('Untersuchungen,' &c., p. 16), and regard the two basal joints as the equivalent of the basal portion of the antenna, or of one of the thoracic limbs; the jointed palpus as the homologue of the inner ramus of the antenna, or the limb proper of one of the thoracic appendages; and the scaphognathite as the homologue of the exopodite of one of the thoracic appendages, or of the antennæ. In all these appendages the exopodite is shorter than the endopodite, unjointed, and set with long hairs, the plumose character of which is well marked. The scaphognathite of the maxilla agrees with the exopodite of the second antenna and of the other appendages in this respect, while the palpus of the maxilla agrees with the endopodite of the second antenna, and with that of the mandible of the *Nauplius* and with the thoracic limbs of the adult *Lucifer*, in consisting of several joints with one or more, usually simple, hairs at each joint.

The inner edges of the basal joints of the maxilla carry cutting hairs, and the second joint is largest. The endopodite carries five long slender hairs which are simple in the earlier and plumose in the later stages. The scaphognathite carries three hairs which are equal and simple in the earlier *Protozoëa*, but plumose in the *Zoëa*, where one is very much longer than the other two.

The structure of this appendage undergoes extremely little change from the time it appears in the *Protozoëa* to maturity. In the Schizopod larva (fig. 52) the second basal joint (2) has become much larger than the first (1), and its cutting hairs are more numerous than before; a small slender plumose hair has made its appearance on the edge of each joint. The endopodite (*en*) is obscurely three-jointed, and the scaphognathite (*sc*) has only two long plumose hairs.

In the adult (fig. 64) the scaphognathite is absent; the endopodite is rudimentary and the second joint of the base (2) is very much wider than the first (1), and has fifteen cutting hairs arranged in three rows, while the first joint has only four very much longer serrated cutting hairs. The basal joint has only one plumose hair as before, but the second joint has one on each side of the blade.

*The second maxilla.*

The second maxilla is present as a bud (fig. 24, *Mx.* 2) in the egg, and it becomes functional in the first *Protozoëa*, and persists without very much change to maturity.

In the first *Protozoëa* (fig. 31) it has a long, many-jointed basal portion (*h*), with slender simple hairs on its inner edge; a two-jointed endopodite (*en*) with three simple hairs on its tip, and two on the second joint; and a small scaphognathite with plumose hairs.

In the last *Zoëa* (fig. 47) the hairs on the inner edge are plumose, and one of the three hairs on the small scaphognathite is much longer than the others.

In the Schizopod stage (fig. 53) the limb is thick and long, the scaphognathite is rudimentary, and the endopodite is small, and has no terminal hairs.

In the adult (fig. 67) the endopodite and all but three of the joints of the basal portion are absent. The first of these (3) is the largest and has a broad edge, with a number of cutting hairs, while the others (2 and 1) are narrow and have three hairs each. All these hairs are simple. The scaphognathite is elongated, and is now about as long as the body of the appendage, to which it is joined by a narrow neck. The inner end has four plumose hairs, three of which are about as long as the appendage, while the fourth was short and apparently broken in all the specimens which I examined. The outer half of the scaphognathite has three short straight plumose hairs on its outer end, and five somewhat longer ones on its inner side.

*The first maxilliped.*

The first maxilliped is represented by a bud in the egg *Nauplius* (fig. 21 *Mp.* 1) and it becomes functional in the first *Protozoëa*, and then consists (fig. 32) of an unjointed exopodite (*ex*) with four long terminal hairs; a four-jointed endopodite (*en*), with three long terminal simple hairs, and a shorter hair springing from the inner edge of each joint; and an obscurely two-jointed basal portion with short simple hairs on its inner edge.

In the *Zoëa* stage (fig. 48) the hairs on the inner edge and on the exopodite are plumose, and the endopodite is long and six-jointed.

In the Schizopod stage (fig. 50, *Mp.* 1) the joints are obscure; the exopodite is nearly as long as the endopodite; all the hairs are plumose, and about equal in length, and there is a double row along the inner edge of the appendage.

In the adult the appendage (fig. 68) is extremely simple, short, stout, two-jointed, flattened on its inner and rounded on its outer surface, with a fringe of short, stout, equal, plumose hairs around the edge of the flattened surface.

*The second maxilliped.*

It is difficult to decide with certainty whether this appendage is represented by a bud in the *Nauplius* or not. If the first pair of buds become the metastoma, as seems probable from their position with reference to the mandibles and from the analogy of the *Euphausia nauplius*, the second pair of maxillipeds are not represented, but if the first pair of buds are the rudimentary first maxillæ the last pair are the second maxillipeds. At any rate the appendages are present in the first *Protozoëa* (fig. 33), and they are essentially like the first pair, but much smaller.

In the last *Zoëa* stage (fig. 49) they are larger, although still smaller than the first, and their inner edges carry only three short hairs which are not plumose.

In the Schizopod stage (fig. 59, *Mp.* 2) a long basal joint carries a four-jointed endopodite and an unjointed exopodite of nearly equal length. The outer half of the exopodite is fringed by fourteen long, simple hairs, and the terminal joint of the endopodite has a few short plumose hairs.

In the next stage the exopodite is absent, and the long six-jointed limb (fig. 70) is bent into the shape which is so characteristic of the adult *Sergestidæ*.

The basal joint (1) is quite short and stout. The next joint (2) is longer and has five plumose hairs, almost as long as the joint, on one side and three on the other.

The next joint (3) is the longest, and carries six plumose hairs. The next (4) is about as long as the second, and the bend in the limb occurs in this joint and between it and the third. It carries ten plumose hairs about as long as those in the other joints, and arranged in a single close rank. The fifth and sixth joints are shorter than any of the others except the first; they are about equal in length, and the fifth carries ten, the sixth six long plumose hairs.

*The third maxilliped.*

This appendage makes its appearance as a bilobed rudiment (figs. 43 and 45, *Mp.* 3), at the end of the *Zoëa* series, and it becomes developed into a Schizopod foot, at the next or first Schizopod stage (fig. 59, *Mp.* 3). A stout basal portion which appears to be two-jointed, carries an unjointed exopodite, and a four-jointed endopodite. The latter branch is the longest, and its tip carries four rather short plumose hairs. The outer half of the exopodite carries fourteen long simple hairs.

At the end of the Schizopod period the limb loses its exopodite entirely, lengthens and becomes a slender six-jointed leg, fringed by a double row of short hairs, as shown in fig. 61, *Mp.* 3.

The history of this appendage in *Lucifer* shows that that there is no reason, except the arbitrary system borrowed from the higher Decapods, for classing this appendage with the mouth parts, instead of with the thoracic limbs.

It appears much later than the first and second pairs of maxillipeds, or at the same time with the thoracic limbs. It agrees with these latter in all its subsequent changes and in its adult structure, and must be regarded as forming one of the thoracic series. I have employed the recognised name, third maxilliped, to prevent confusion, but the appendage is in no sense a mouth part. In fact, the only reason for holding that the missing appendage in *Lucifer* is the fifth pereiopod, instead of the last maxilliped, is the tacit assumption that the appendages must follow a definite serial order from in front backwards. We do not know that this assumption is justifiable in all cases, and it is therefore perfectly possible that the appendage which is usually called the third maxilliped of *Lucifer* may really be the first pereioped. I think the probability is in favour of the accepted homology, but the use of the term "third maxilliped" in the present paper for the appendage in question must not be regarded as evidence that the homology is accepted without question.

*The pereiopods.*

At the end of the *Zoëa* series four pairs of pereiopods, the first, second, third, and fourth, are represented by buds (figs. 43 and 45), while the fifth is entirely absent, as DANA pointed out in the 'Report on the Crustacea collected by the United States Exploring Expedition,' p. 634. WILLEMÖES-SUHM (Proc. Roy. Soc., vol. 24, p. 134), calls attention to the same fact: the total absence of this somite at all stages of development. In the Schizopod stage each of these appendages is biramous (fig. 59), and similar to the last maxilliped, although the first three pairs (fig. 59, *Pr.* 1, *Pr.* 2, and *Pr.* 3) are longer.

At the end of the Schizopod series of stages the entire fourth pair and the exopodites of the other three pairs disappear, and the endopodites lengthen to form the long slender limbs of the adult (fig. 61, *Pr.* 1, *Pr.* 2, and *Pr.* 3). They are four-jointed, with a double row of short hairs along the anterior edge, and the first is only half as long as the second and third, which are nearly equal, and almost as long as the carapace and neck. The third ends in a short, curved hairy claw, too small to be shown in the figure.

*The first abdominal appendage.*

This is present as a rudimentary bud at the end of the Schizopod series, but does not become functional until the *Lucifer* form is reached. In the young it consists of a long unjointed base, and a single pointed tip, fringed with swimming hairs (fig. 61, *Pl.* 1). In older specimens the basal portion divides into two joints, and in the young male or the young or mature female the appendage has the form shown in fig. 74. As the male approaches maturity a small process, shown in fig. 76,

appears on its anterior face, and becomes modified in the mature male into the clasping organ (fig. 75, *e*), while a second process (*d*) appears a little nearer the tip of the limb.

*The second abdominal appendage.*

This appears at the same time with the first, and developes two terminal branches. In the mature male a third shorter one is added.

*The third, fourth, and fifth abdominal appendages.*

These all develop at the same time with the first and second; they have two terminal branches and are alike in both sexes.

*The sixth abdominal appendage.*

This is present as a rudiment in the last "*Zoëa*," and it becomes fully developed in the first Schizopod larva.

It consists of a basal joint which carries a long, wide, and flat exopodite, and a narrower shorter endopodite.

In the young and in the mature female the outer end of the exopodite is rounded, but it is nearly square in the mature male.

*The labrum.*

The labrum is large and conspicuous in the *Nauplius*, but it has no spine. The spine is present from the first *Protozoëa* stage to the last Schizopod stage, but it is absent in the adult.

*The compound eyes.*

These make their appearance as rudiments in the last *Protozoëa*, but they are not perfectly developed or stalked until the last Schizopod stage. The homology of the stalked eyes of the Malacostracan has been a matter of some uncertainty. They are usually enumerated in the list of appendages, and the typical Crustacean is supposed to have a corresponding somite. Claus has pointed out ("Zur. Kenntniss der Malacostrakenlarva," Würzb. Zeitschr. ii., 1861. p. 33) that no especial taxonomic importance can be attached to their presence or absence; and their mode of origin in *Lucifer* certainly gives no support to the view that they have been produced, like the mandibles, by the gradual specialisation of a pair of ordinary appendages. They do not resemble ordinary appendages at any stage, but are formed directly, and the fact that the period of their development is spread over several moults renders their history quite different from that of the appendages. As I shall show further on,

serially homologous organs do not necessarily owe their resemblances to inheritance from the unspecialised organs of a remote ancestor, and I think that the presence of a distinct ocular segment in *Squilla* compels us to recognise an homology between the stalked eye and an ordinary appendage, although it is no doubt true that all the groups in which stalked eyes occur cannot be traced back to a common stalked-eyed ancestor, and also true that the stalked eyes themselves cannot be traced back to ordinary appendages.

### *The ocellus.*

This is present from the first *Nauplius* stage to the end of the Schizopod series.

### *Explanation of Table I.*

This table is designed to show at a single view the condition of each appendage at each stage of development.

For convenience I have included the compound eyes, the ocellus, and the labrum, but do not wish to imply that these structures are or are not homologous with ordinary appendages, and I have omitted the metastoma, although I have no doubt that this should be included in a list of the appendages.

In the table the word "same" indicates that the condition of the appendage is the same as it was at an earlier stage, and does not refer to other appendages in the same vertical line.

TABLE I.—Comparative table to show the history of the appendages of *Lucifer*.

| | Nauplius. | First *Protozoëa* or *Erichthina* Stage. | Last *Zoëa*. | First Schizopod or *Sceletina* Stage. | Last Schizopod. | Young of both sexes and adult female. | Adult male. |
|---|---|---|---|---|---|---|---|
| Compound eye | Absent | Same | Not stalked. | Stalked | Same | Same | Same |
| Ocellus | Present | Same | Same | Same | Same | Absent | Absent |
| First antenna | Has nauplius form | Same | Same | Adult form, but rudimentary | Adult form | Same | Same |
| Second antenna | Has nauplius form | Same | Same | Rudimentary | Adult form | Same | Same |
| Labrum | No spine | Spine | Same | Same | Same | No spine | Same |
| Mandible | Biramous limb | Adult form | Same | Same | Same | Same | Same |
| First maxilla | Bud | Biramous | Same | Same | Same | Seaphoguathite absent, endopodite rudimentary | Same |
| Second maxilla | Bud | Biramous | Same | Endopodite and seaphognathite rudimentary | Same | Endopodite absent, seaphognathite large | Same |
| First maxilliped | Bud | Biramous | Same | Same | Same | Rami absent | Same |
| Second maxilliped | Bud | Biramous | Same | Same | Same | Exopodite absent | Same |
| Third maxilliped | Absent | Same | Bud | Biramous | Same | Exopodite absent | Same |
| First pereiopod | Absent | Same | Bud | Biramous | Same | Exopodite absent | Same |
| Second pereiopod | Absent | Same | Bud | Biramous | Same | Exopodite absent | Same |
| Third pereiopod | Absent | Same | Bud | Biramous | Same | Exopodite absent | Same |
| Fourth pereiopod | Absent | Same | Bud | Biramous | Same | Absent | Same |
| Fifth pereiopod | Absent | Same | Same | Same | Same | Same | Same |
| First pleopod | Absent | Same | Same | Same | Bud | One ramus | Clasper |
| Second pleopod | Absent | Same | Same | Same | Bud | Two rami | Three rami |
| Third pleopod | Absent | Same | Same | Same | Bud | Two rami | Same |
| Fourth pleopod | Absent | Same | Same | Same | Bud | Two rami | Same |
| Fifth pleopod | Absent | Same | Same | Same | Bud | Two rami | Same |
| Sixth pleopod | Absent | Same | Bud | Biramous | Same | Exopodite round at tip | Exopodite square at tip |

## V. The Metamorphosis of Acetes.

While I was studying the development of *Lucifer*, I found during the month of September a few specimens of the very similar larva which is shown from above in Plate 9, fig. 79, and from the side in fig. 78.

Several specimens were placed by themselves in tumblers of sea-water, where they passed through the stages shown in Plate 11, figs. 84, 85, and 90. Only one of my specimens reached this last stage, and as this one moulted on the last day of the season I was not able to trace it any further, and as I collected no adult specimens of the same kind, its precise systematic position must at present remain in some uncertainty. The close similarity which I shall point out between its larval stages and those of *Lucifer* and *Sergestes* renders it very probable that it is a Sergestid, and the analogy of these forms also indicates that the larva shown in fig. 90 has in all probability nearly or quite attained to the mature form. This larva differs from the other two forms in the possession of small claws at the tips of the last three pairs of pereiopods, and as this is characteristic of Milne-Edwards' genus *Acetes*, and only three genera of Sergestidæ—*Lucifer*, *Acetes*, and *Sergestes*—have been described, I think we may conclude that we have to do with the development of an American species of this genus. At any rate, whatever the systematic position of the adult may be, the fact that the *Protozoëa* is in most respects intermediate between the simple *Protozoëa* of *Lucifer* and the extremely modified *Protozoëa* of *Sergestes*, gives this form so much interest that it seemed best, for the sake of comparison, to embody all that I was able to learn about its metamorphosis in the present paper.

At the earliest stage which was observed, the larva (figs. 77, 78, and 79) is a "*Zoëa*" $\frac{67}{1000}$ inch long, and a comparison of fig. 79 with fig. 44, or of fig. 77 with fig. 43, will show that it is essentially like the last *Zoëa* of *Lucifer*, although the minor differences are both numerous and conspicuous.

The number of somites and appendages is alike in both forms, and the appendages are alike in most respects, although each one of them shows distinctive characteristics of its own.

The carapace (fig. 79) makes about one-half the length of the body, and it is much more flattened than it is in *Lucifer*. It has a rostrum (*R*) and a median dorsal spine, but the postero-lateral spines (*sp.*) point outwards and backwards, instead of directly backwards, and there are a pair of anterior spines as long as the rostrum, projecting over the eyes. The two large pigment-spots which give such a characteristic appearance to the carapace of *Lucifer* are entirely absent, and the thoracic segments and appendages are covered by its posterior edge.

The eyes are mounted upon distinct stalks, while they are sessile in *Lucifer* at the same stage.

The abdominal somites are short and wide, and coloured by bright-red pigment-spots, and their lower edges are produced into strong projecting spines.

The telson is deeply cleft, and its halves diverge from each other like a swallow's tail feathers, so that the posterior ends of the rudimentary swimmerets are visible between them in a dorsal view, as shown in figs. 77, 78, and 79. The spines on the telson are similar in arrangement to those of *Lucifer*, but much longer.

A comparison of the Lucifer *Zoëa* (fig. 44), the Acetes *Zoëa* (fig. 79), and the Sergestes *Zoëa* (CLAUS's 'Crustacean-System,' taf. vi., fig. 1) at the same stage of development, brings out the extremely interesting fact that the *Acetes* larva stands between the very simple *Zoëa* of *Lucifer* and the remarkably complicated *Elaphocaris* larva of *Sergestes* in nearly every feature in which the two differ. In *Lucifer* the eyes are sessile; in *Acetes* they have short stalks; and in *Sergestes* the stalks are very long.

In *Lucifer* the spines over the eyes are absent; in *Acetes* they are present and simple; and in *Sergestes* they are very long and compound.

In *Lucifer* the postero-lateral spines are parallel to the long axis of the body; in *Acetes* they are oblique, so that they project a little beyond the outline of the body; and in *Sergestes* they are at right angles to the long axis, and compound.

The carapace, including the rostrum, makes about one-third of the total length of the body of the Lucifer *Zoëa;* about one-half of that of the Acetes *Zoëa;* and more than two-thirds of the total length of the Sergestes *Zoëa*. The abdominal somites of the Acetes *Zoëa* are shorter and wider than those of the Lucifer *Zoëa*, and this change is carried still further in the Sergestes *Zoëa*. In the Lucifer *Zoëa* the sixth abdominal somite is the only one which has ventral spines, and these point backwards. All the abdominal somites of *Acetes* have spines, and they point backwards and a little outwards, while in *Sergestes* they all point directly outwards.

The telson is slightly notched in *Lucifer;* deeply forked in *Acetes;* and in *Sergestes* the prongs of the fork diverge so much as to form a right angle.

These facts are extremely interesting, as they seem to show that the *Elaphocaris* is a larva essentially like that of *Lucifer*, which has passed through a remarkable process of secondary modification, resulting in the acceleration of the development of the eyes, and the production of a forked telson, and a very spiny body. The larva of *Acetes* has been modified in the same direction but to a much less degree. It may be asked why we are to assume that the Lucifer *Zoëa* is the primitive form, and the *Elaphocaris* larva the secondary modification rather than the reverse; but a little thought will show that the distinctive features of the *Elaphocaris* stand in direct relation to the environment, as weapons of defence, sense organs, or locomotor apparatus, while the distinctive marks of the Lucifer *Zoëa* are features of general or typical resemblance to the corresponding larva of *Euphausia* and *Penæus*.

I did not succeed in finding the *Protozoëa* from which the *Zoëa* shown in fig. 79 is derived, but I think it extremely probable that future research will show that an unknown larva which has been figured by DOHRN and CLAUS is the *Protozoëa* of *Acetes*, or else of a new closely-related genus of the Sergestidæ.

In his "Untersuchungen über Bau und Entwickelung der Anthropoden" (Zeit. f.

Wiss. Zool., xxi., 1871), DOHRN describes the "Larve eines unbekannten Krebses" from the Indian Ocean (p. 377), which is shown in his plates 29 and 30, figs. 62 to 67. In his 'Crustacean-System' (taf. iv., figs. 2 to 7) CLAUS gives much more satisfactory figures of what appears to be the same larva, and speaks of it as a "Phyllopodenähnlichen Protozoëa unbekannter Herkunft." Its close resemblance to the *Protozoëa* of *Lucifer* renders it extremely probable that it is the *Protozoëa* of a Sergestid, and as the *Protozoëa* of *Lucifer* and that of *Sergestes* are known, this must be the larva of *Acetes*, or of some closely-related unknown form.

The carapace is nearly smooth, rounded, and there is no trace of a rostrum, and it makes more than three-quarters of the total length of the body.

The compound eyes are present and well developed, but they are sessile, and there is no indication of the stalk. The first antenna is seven-jointed, and the two terminal joints are thin and long.

The second antenna is nearly twice as long as the first, and very thick. Its short stout basal portion consists of two joints, and carries a short two-jointed exopodite, with three long terminal non-plumose swimming hairs, and a very large twelve-jointed endopodite with a long swimming hair at each joint.

CLAUS's figures show that the appendages at the back of the antennæ are very much like those of *Lucifer*, and the same ones are present; that is, the mandibles, first and second maxillæ, and first and second maxillipeds.

The hind body is segmented, and ends in a broad, flat, deeply-cleft telson, with six pairs of irregularly plumose hairs, the third pair very much longer and thicker than the others.

A comparison of CLAUS's figure with fig. 27 of this paper will show that most of the differences between this unknown larva and the first *Protozoëa* of *Lucifer* are of the same kind as the differences between the Acetes *Zoëa* (fig. 79) and the corresponding stage of *Lucifer* (fig. 44).

At a time when the eyes of *Lucifer* are rudimentary and sessile they are perfect and stalked in *Acetes*, and at a time when they are entirely absent in *Lucifer* DOHRN's larva has them sessile and rudimentary but distinct.

The *Zoëa* of *Acetes*, like this larva, has its telson deeply forked; its hairs are plumose, and the third is much longer than the others. These resemblances, and the great length of the carapace, render it very probable that this unknown larva is the *Protozoëa* of *Acetes*.

I will now continue my description of the appendages of the *Zoëa*.

The first antenna (fig. 77, *A*) is uniramous, and it consists of a long, cylindrical, two-jointed shaft, and a single short flagellum, which shows obscure traces of a division into three joints. The basal joint of the shaft is a little more than half as long as the second joint, and it carries a single short sharp hair on the inner side of its distal end. The second joint has two much longer hairs on its distal end, and one about half way between its ends. The flagellum makes about one-fifth of the total length of the

appendage, and it carries four terminal hairs, two of them about as long as those on the terminal joint of the shaft, and two nearly three times as long.

The second antenna is the chief locomotor organ, and (as shown in fig. 77, *An*) it consists of a thick two-jointed basal portion, which carries a two-jointed exopodite (*ex*) and a ten-jointed endopodite (*en*).

The proximal joint of the exopodite is about twice as long as the terminal joint, and it carries two long hairs on its outer end, and two more near the base. The terminal joint has, at its tip, one short hair, and four which are about as long as the limb. The endopodite consists of four short rings, and a series of six joints like those of the corresponding organ of the *Nauplius*, *Protozoëa*, and *Zoëa* of *Lucifer*. The terminal joint carries four, and each of the five other joints one long swimming hair, and none of these hairs are plumose.

On the basal portion of the appendage there is a large bright-red pigment-spot, which forks and runs along the exopodite and endopodite, about half way to their tips.

The labrum (fig. 77, *L*) is smaller than that of *Lucifer*, with a spine and a large red pigment-spot.

The mandible (fig. 77, *M*, and fig. 80) has small irregular denticles along its cutting edge, and these reach to the tip of the long tooth which occupies the posterior angle of the blade. The mandibles of two specimens were dissected out, and in each case there was a little hairy pad (*m*) upon the posterior surface. It could also be seen in the entire animal (as shown in fig. 77). It is possible that this pad is the mandibular palpus, but it seems much more probable that it is half of the lower lip or metastoma, for no palpus is present on the mandible of *Lucifer*.

The first maxilla (fig. 77, *Mx.* 1, and fig. 81) is quite different from that of *Lucifer* (fig. 46) at the same stage, but the difference is in minor points, and there is essential agreement in general structure. The two basal joints or blades are long and slender, and their hairs are also longer and thinner than they are in *Lucifer*. The endopodite (*en*) is placed nearly at right angles to the base, and is distinctly three-jointed. It carries five hairs as it does in *Lucifer*, and they are similarly placed, but longer. The three hairs on the scaphognathite are about equal in length, and the plumules on their sides are short and irregular.

The second maxilla (fig. 77, *Mx.* 2, and fig. 82) is much like that of the Lucifer *Zoëa* (fig. 47), but the three hairs at the tip are more than twice as long as those on the inner edge of the appendage, and they are irregularly plumose, while they are simple in *Lucifer*.

The first maxilliped (fig. 77, *Mp.* 1, and fig. 83) differs from that of *Lucifer* (fig. 48) in the same way, and the exopodite carries seven instead of four hairs, and these are as long as the appendage, and two-jointed.

The second maxilliped (fig. 77, *Mp.* 2) is about as long as the first, but it does not seem to be of much functional importance. It is usually carried stretched back along

the hind body, as shown in the figure, and its hairs are short. As in *Lucifer* at the same stage, the exopodite is as long as the endopodite.

The third pair of maxillipeds, and the first, second, third, and fourth pairs of thoracic limbs are represented by buds, as in *Lucifer* at the same stage. The bud for the third maxilliped (fig. 77, *Mp.* 3) is bilobed, longer than the others, and it points backwards outside the other buds. The buds for the first three pairs of periopods are bilobed, in contact on the median line, and about equal in size. Those for the fourth pair are much smaller, and are hidden in a ventral view by the buds for the third pair, but they can be seen in side view (as shown at *T* 4 in fig. 78). There is no trace of the fifth pair of pereipods either at this or at any later stage. CLAUS figures buds for the fifth pair in the *Zoëa* of *Sergestes*, and also in the next or *Acanthosoma* stage of *Sergestes;* but the study of the *Zoëa* of *Acetes* shows even more satisfactorily than is the case in *Lucifer* that these appendages are entirely absent, and it seems safe to believe that this is the case in *Sergestes* also until the larva of the latter has been carefully examined with reference to this particular point.

The abdominal appendages, with the exception of the fifth pair, are entirely absent; but each abdominal somite has a pair of long ventral spines. The swimmerets are represented by long bilobed buds, which project beyond the fork or notch in the telson. The abdominal ganglia are very much more conspicuous than they are in *Lucifer*.

The distribution of pigment is somewhat different from what we find in the Lucifer *Zoëa*, and nearly all the pigment-spots are bright-red. There is a large spot of red and one of reddish-yellow on the eye stalk, a red spot on the labrum, a large red and very dendritic spot on the second antenna, red spots on the dorsal surface of the posterior edge of the third, fourth, and fifth abdominal somites on the median line; red spots on the ventral surface of the first, second, and third at the bases of the spines; a red and a brown spot at the base of the spine on the fifth; a brown spot at the base of the spine on the sixth, and a red spot on the base of the swimmeret. The anal spots are large and bright-red.

On September 20th I found several specimens of the stage which has just been described. Fig. 79 was made from one of them, which was then placed in a glass of water by itself, and the next day it was found to be moulting. In the evening the moult was found to be finished, and the larva was swimming actively. The drawing given in fig. 84 was made from it without injuring it, and later stages were also drawn from the same specimen.

The larva, $\frac{79}{1000}$ inch long, has undergone very great change, and although it is an *Acanthosoma*, it presents many important differences from both *Lucifer* and *Sergestes*.

The abdomen has lengthened so that the carapace makes less than one-third the total length of the body, and the dorsal and postero-lateral spines have disappeared.

The abdominal spines stand out from the body, and the swimmerets have become the chief locomotor organs. The spine has disappeared from the labrum; the two pairs of antennæ have changed from the larval to the adult form; the endopodite of the fourth pereiopod, and the first three pairs of pleopods are represented by long buds.

The first antenna (fig. 84, *A*) consists of a three-jointed shaft about as long as the carapace, and two terminal flagella. The basal joint of the shaft makes half the total length of the appendage, and the other two are about equal to each other. On the inner edge of the distal two-thirds of the shaft there are eight long, similar equidistant, plumose hairs, and there are two short spines on the outer edge. The inner flagellum is short, and carries one long slender terminal hair. The outer one is more than twice as long, and carries two thick sensory hairs.

The exopodite of the second antenna (fig. 84, *ex*) has become a scale, only one-third as long as the endopodite, which is now a ten-jointed flagellum about as long as the carapace.

The second and third maxillipeds (fig. 84, *Mp.* 2 and *Mp.* 3) and the first, second and third pereipods (fig. 84, *T* 1, *T* 2, and *T* 3), are Schizoped-like, but they are of very slight functional importance, and their endopodites are folded forwards on the ventral surface, like the maxillipeds of *Squilla*, so that it is impossible to study the mouth parts without dissection. The endopodite of the fourth pereiopod has entirely disappeared, and the limb is represented only by its exopodite. The five exopodites are about alike, and they all end in long slender swimming hairs: those of the four pereiopods (*T* 1 *ex*, *T* 2 *ex*, *T* 3 *ex*, and *T* 4 *ex*) are bent outwards and upwards towards the dorsal surface, as in the maxillipeds of a Crab *Zoëa*, but those of the second and third maxillipeds (*Mp.* 2 *ex* and *Mp.* 3 *ex*) are more nearly parallel to the endopodites. The endopodite of the second maxilliped (*Mp.* 2) is free and movable, but those of the third maxillipeds (*Mp.* 3) and of the first, second, and third pereiopods are covered by a delicate cuticle, and are almost immovable.

I did not actually witness the next moult, but four days later the larva, $\frac{80}{1000}$ inch long, was in the stage shown in fig. 85. The exopodites of the thoracic limbs have become reduced to rudiments, the limbs themselves have stretched out and are now functional, as are the three pairs of abdominal feet.

The first antenna (fig. 86) has not changed much, but its base is swollen and the otocyst has appeared.

The second antenna is now half as long as the whole body, its flagellum is ten-jointed, and red pigment has appeared at its base and tip (fig. 87). The outer end of the scale carries nine long plumose hairs arranged on the tip and inner edge.

The second maxilliped (fig. 88, *Mp.* 2) is bent into a knee, and is fringed by sixteen plumose hairs. Its exopodite is rudimentary, but longer than in any of the appendages which follow.

The third maxilliped (fig. 88, *Mp.* 3) is long, slender, six-jointed, with a rudimentary endopodite.

The other three limbs (fig. 88, *T* 1, *T* 2, *T* 3) are six-jointed and they end in enlarged chelæ. The first is the shortest; the second is about as long as the third maxilliped, and the third is still longer. The fourth is now represented only by a small rudiment and a ganglion; and the fifth is entirely absent, as it has been at all stages.

The three pairs of pleopods are alike in structure, and each consists of two joints about equal in length (fig. 89). The outer half of the terminal joint is toothed and carries six pairs of long slender non-plumose hairs, so arranged as to form a paddle.

The rostrum (fig. 85) is long and curved, and it has a single secondary spine in its upper surface. A pair of very small spines have also appeared at its base.

This specimen had nearly completed its moult into the stage shown in fig. 90 on the last day of my stay at the seashore—five days after fig. 85 was drawn.

Fig. 90 was drawn from another specimen, $\frac{15}{100}$ inch long, which was captured at the surface on September 25th.

The eye-stalks are long and very movable, the flagellum of the second antenna is considerably longer than the body, the five pairs of thoracic limbs have developed gills, and the fourth and fifth pleopods have appeared; but in other respects the structure is nearly as it was in the preceding stage. The endopodites of the maxillipeds are pointed, but those of the three pereiopods end in rudimentary chelæ. The endopodite of the third pereiopod is much longer and thicker than the others, and its tip reaches nearly to the rostrum.

The buds for the first three pairs of pleopods are long, obscurely jointed, and they meet each other on the median line. There are as yet no traces of the fourth and fifth pairs. The spines on the abdominal somites are long and sharp. Those on the first three somites point outwards and forwards, those on the fourth point almost directly outwards, and those on the fifth outwards and backwards. The sixth abdominal somite has lengthened, and is now about as long as those of the others. The telson is short and shield-shaped, with two pairs of long and one pair of very short spines, and the swimmerets are perfectly formed and fringed with long plumose swimming hairs.

The exopodite is long, narrow, with a smooth outer edge which ends in a tooth, and a rounded point. It carries fifteen hairs: ten on the inner edge, two on the tip, and three between the tip and the tooth. The endopodite is nearly as long and wide as the exopodite, and it carries nineteen hairs: two at the end, eight on the outer, and nine on the inner edge.

The ocellus is still present, and the pigment-spots have nearly the same arrangement as before, but some of them are now yellow or green instead of red.

The eye-stalk is about as it was before, and the ocellus is still present and double. As regards the more minute structure of the appendages the first antennæ are now about as long as the carapace, and most of the increased length is in the flagellum, which now consists of seven joints. The secondary flagellum is still quite short. The shaft of the antenna is three-jointed, as before, but the basal joint is much lengthened, and now makes more than half the total length. The auditory organ at its base is now very conspicuous, and the inner edge of the shaft carries eleven hairs instead of six; five of these are on the basal joint, three on the second joint, and three on the third.

The scale of the second antenna has lengthened and is now more than half as long as

the first antenna, including the flagellum. Its inner end carries eight, and its tip three hairs, and the outer edge of the tip is toothed. The swollen base of the flagellum of the second antenna carries a large red pigment-spot, and the flagellum, which is considerably longer than the body of the animal, is also marked by bright-red pigment throughout the greater part of its length.

The second maxilliped has become completely bent upon itself, and it bears a close resemblance to that of the adult *Lucifer*, although it carries a gill, as do the second maxillipeds and the three pairs of thoracic limbs. All traces of the exopodites have disappeared from all these appendages, but their structure and comparative length are about as before.

The first, second, and third pairs of abdominal feet have increased in length, and the first is now almost as long as the last thoracic limb. The second is a little shorter; the third is still shorter, and has acquired a second terminal branch, which is as yet rudimentary.

The fourth and fifth pleopods, which have now made their appearance, are much smaller than the others, and each has one large and one small terminal branch.

The swimmerets and telson are very similar to those of the immature *Lucifer*, although the telson is shorter and wider. The exopodite has fifteen hairs on its inner edge, two on its rounded tip, and four between the tip and the tooth. The endopodite has nineteen hairs. The surface of the carapace is finely punctated, and the rostrum has no secondary spine. The spine has disappeared from the first abdominal somite, and the one on the third somite is longer than any of the others. The dorsal surface of the third somite is bent, so that the abdomen is no longer perfectly straight. Large conspicuous red pigment-spots have appeared on the lower edges of the second, third, fourth, and fifth abdominal somites.

As the series of drawings which I have given was made from such a small number of specimens, I am unable to contribute much information as to the changes of the mouth parts, and must leave this, as well as the exact determination of the adult form and systematic position of the species, to future research.

In his 'Facts for Darwin' Fr. Müller has figured a larva (fig. 33) which is extremely like, if not identical with the one shown in fig. 90, and he regards it as the young of a Prawn, closely related to *Penæus*. Claus has suggested ('Crustacean-System,' p. 35) that it is much more likely to prove to be a young Sergestid than a Prawn, and the facts regarding its metamorphosis which I have given above, certainly seem to point in the same direction. An earlier stage of development is given in Fr. Müller's fig. 32, and a comparison with my fig. 84 will show that the same larva at an earlier stage might, when crushed by a cover glass, present very much the same appearance as this larva. If they are the same Fr. Müller is certainly mistaken in his statement that fig. 33 follows directly after fig. 32, without the intervention of a Schizopod stage, for the metamorphosis is really quite complicated, and a true Schizopod stage exists, although it is of extremely short duration.

## VI.—Relation between the Larvæ of Lucifer, Acetes, Sergestes, Penæus, and Euphausia, and the Significance of the Decapod Zoëa and the Crustacean Nauplius.

The general significance of the peculiar type of Decapod metamorphosis, of which *Lucifer* is now the most thoroughly known illustration, has been discussed with the greatest ability and knowledge of the facts by Claus in his 'Untersuchungen zur Erforschung der Genealogischen Grundlage des Crustacean-Systems.' My own acquaintance with the phenomena of Crustacean morphology in general is very far from being sufficiently extended and minute to qualify me for a critical discussion of this work; but while the facts in the life-history of *Lucifer* seem to tend to a similar conclusion, and even to place it upon a much firmer basis than before, they also indicate that Claus's views cannot receive unqualified acceptance in their present shape.

I shall not venture at present upon the broader aspects of the question, but I wish to draw attention to the resemblances and differences between the various larval stages of *Lucifer* and those of a few closely-related forms. The materials which are at present available for a comparison of this kind are extremely scanty, for there is no other closely-related form in which all stages, from the egg to the adult, have been actually traced in a single species by rearing captive specimens.

### *Comparison of* Lucifer *and* Acetes.

The genus which shows the closest similarity to *Lucifer* is *Acetes*, but in this case we are ignorant of both the early and the later stages. During the last "*Zoëa*" stage the resemblance between the two forms is well marked, and is shown in such features as the similarity in the shape of the carapace and hind body; in the length and structure of the two pairs of antennæ; in the mode of locomotion; by rowing with the antennæ; in the presence of an ocellus; the presence of a spine on the labrum; the close similarity of the mouth parts and maxillipeds; the rudimentary structure of the thoracic limbs and swimmerets; the total absence of the fifth thoracic somite; and the absence of the first five pairs of pereiopods. Notwithstanding these resemblances the differences are quite conspicuous. The eye is sessile in *Lucifer*, stalked in *Acetes*. The shaft of the first antenna is one-jointed in *Lucifer*, two-jointed in *Acetes*. The endopodite of the second antenna has two basal rings in *Lucifer*, four in *Acetes*. The two lobes of the metastoma are conspicuous in *Acetes*, and could not be made out at all in *Lucifer*. The abdominal somites are rounded in *Lucifer*, and spiny in *Acetes;* and the telson is deeply forked in the latter, slightly notched in the former. In a word, the resemblances between the two are general rather than detailed, and the differences are specific differences of the same character as those between closely related adult animals. A comparison of column 2 of Table V. with column 1 will show these resemblances and differences in tabular form.

If we assume the correctness of the extremely probable assumption that Dohrn's and Claus's unknown larva is the earliest *Protozoëa* of *Acetes*, the resemblances between it and the corresponding larva of *Lucifer* (compare fig. 27 with Claus, fig. 2, taf. iv.) are much greater than they are at a later stage. The chief differences are the presence in *Acetes* of rudimentary compound eyes; the great length of the carapace; the absence of a rostrum and spines; the great number of joints in the first and second antenna, and the difference in the length of these two appendages; the deep notch in the telson. The close similarity between the two larvæ at this stage will be seen by comparing column 1 of Table IV. with column 2.

After the moult which ends the *Zoëa* series the differences between the *Acetes* larva (fig. 89) and the *Lucifer* larva (fig. 53) become much greater, although they do not obscure the fundamental similarity between the two forms. In each of them the carapace makes less than one-third the total length of the body, and it has a rostrum and two antero-lateral, but no postero-lateral or dorsal spines. The first antenna has lost its swimming hairs, and has developed one flagellum in each form and two in *Acetes*. In both forms a series of long plumose hairs has appeared on the inner edge of the shaft of the appendage. In both forms the second antenna has lost its locomotor function and assumed the adult form, but it is rudimentary in *Lucifer* and well developed in *Acetes*.

The ocellus is present and the eye stalked and movable in both.

The fifth thoracic somite and its appendages are entirely wanting in both forms. The fourth is biramous in *Lucifer*, and similar to the ones before it, but in *Acetes* the limb proper has disappeared and the appendage is represented only by an exopodite. The second and third pairs of maxillipeds, and the first, second, and third pairs of pereiopods are essentially alike in structure in both forms, but in *Acetes* the endopodites are rudimentary, covered by a cuticle, and functionless. The swimmerets are present and very similar in the two forms, but the other abdominal appendages are absent in *Lucifer*, while the first, second, and third pairs are developed, but rudimentary in *Acetes*. The abdominal somites have acquired ventral spines in both forms, but these are very small in *Lucifer* and long and prominent in *Acetes*. The telson is long and narrow in *Lucifer* and short and wide in *Acetes*. The relation between the two forms at this stage of development will be seen by a comparison of columns 1 and 2 of Table VI.

The later history of the two genera can hardly be divided into parallel stages. *Lucifer* keeps all its Schizopod limbs for at least two more moults, and as shown in fig. 54, acquires the rudiments of all the abdominal feet at one time, and before the fourth pair of thoracic limbs and the exopodites of the others and of the maxillipeds disappear, while *Acetes* (fig. 85) loses its exopodites at once, and the maxillipeds, thoracic limbs, and antennæ become like those of an adult Sergestid some time before the appearance of the five pairs of pleopods; and these do not appear together, but in two sets.

It is interesting to note that although the changes which the two forms undergo

at successive moults do not admit of exact comparison with each other; the outcome, after a few moults, is almost exactly the same, as will be seen by a comparison of fig. 60 with fig. 90.

The number and character of the somites and appendages is now the same, and while the two forms differ greatly in outline and proportion, the young *Acetes* is essentially like the young *Lucifer*, except in the length of the flagellum of the second antenna, the presence of chelæ on the thoracic limbs, the presence of gills, and the absence of a "neck." The outcome of the process of development is alike, but the paths followed diverge from each other to converge again at this stage.

### *Comparison of* Lucifer *and* Sergestes.

The metamorphosis of *Sergestes* is more like that of *Lucifer* than is the case with any other known Crustacean except *Acetes*, but our knowledge of the development of *Sergestes* is incomplete, and we have no assurance that the various stages which have been described belong to the same species.

In 1870, Dohrn described a remarkable larva ("Untersuchungen über Bau und Entwickelung der Decapoden, No. 10, Beiträge zur Kenntniss der Malacostraken und ihrer Larven, Part 4, Beschreibung einer neuen Decapoden-Larve," Zeit. f. Wiss. Zool., xx., p. 607) which he collected at the surface at Messina, and which he was unable to refer to any adult form. He proposed for this larva the provisional name *Elaphocaris*. *Elaphocaris* is a *Zoëa* which so far as its appendages are concerned does not differ much from the last *Zoëa* of *Lucifer*, but its abdomen is very spiny, and the spines on the carapace are drawn out so that each one of them is nearly half as long as the body, and they are fringed with rows of long secondary spines which are hooked at their tips, and so arranged as to give to the body a very grotesque appearance, and the larva does not, at first sight, show any similarity to the simple *Erichthina* larva of *Lucifer*.

Claus had several years before described ("Ueber einige Schizopoden und niedere Malacostraken Messinas," Zeit. f. Wiss. Zool., xiii., 1863) a larval Crustacean with swimmerets, biramous thoracic limbs, and a very spiny body, which he calls an *Acanthosoma*. This same larva, or a very closely related form, had been figured and described nearly twenty-five years before by Dana ('Crustacea,' p. 664, plate 44, fig. 5) as *Sceletina armata*.

In the same paper Claus gives a figure of a young Crustacean, which had previously been described by Leuckart under the name of *Mastigopus*, and shows that it is in all probability a young *Sergestes*.

In his 'Untersuchungen zur Erforschung,' &c., he describes an *Elaphocaris* at a much younger stage than Dohrn's figure, and shows that this larva, Dohrn's *Elaphocaris*, his own *Acanthosoma*, and Leuckart's *Mastigopus* are successive stages in the development of *Sergestes*.

From independent researches in the South Pacific, Willemöes-Suhm also ascertained (Proc. Royal Soc., Dec. 9, 1875, p. 133) that *Elaphocaris* is the larva of *Sergestes*, and he traced its development through the *Acanthosoma* stage, which, from its resemblance to *Amphion*, he calls the *Amphion* stage.

These various observations, and especially those by Claus, give us a pretty complete acquaintance with the metamorphosis of *Sergestes* from the first *Protozoëa* stage to maturity.

The first *Protozoëa* (Claus, 'Untersuchungen,' taf. v., fig. 1) has, like the *Protozoëa* of *Lucifer*, locomotor antennæ, a spine on the labrum, a partially segmented hind body, and a very spiny telson. The mandibles, first and second maxillæ, and first and second maxillipeds are like those of the corresponding *Lucifer* larva. In addition to the spiny carapace it presents the following conspicuous differences from the *Lucifer* larva. The eyes are stalked, movable, and compound. The first antenna has seven joints. The endopodite of the second antenna has no small rings at its base. There is a third pair of maxillipeds. Five thoracic somites are represented in the figure. The telson is very deeply cleft. The relation between the larva and the first *Protozoëa* of *Lucifer* will be seen by a comparison of columns 1 and 3 of Table IV.

The next stage which Claus describes (taf. vi., fig. 1) is no doubt separated from the first by one or more intermediate stages. The rostrum has developed a pair of long secondary compound spines at its base, which do not correspond to anything in the corresponding larvæ of *Acetes* and *Lucifer*.

The thoracic limbs are represented by *five* pairs of rudimentary bilobed buds. There are five free abdominal somites without appendages, and the sixth and telson are represented by an unsegmented region, which carries a pair of long bilobed pouches, the rudimentary swimmerets.

The relation between *Elaphocaris* and the corresponding larvæ of *Acetes* and *Lucifer* may be understood by a comparison of column 3 of Table V. with columns 1 and 2.

In the next or *Acanthosoma* stage ('Untersuchungen,' taf. v., fig. 6) the two pairs of antennæ assume the adult form, and the thoracic limbs and swimmerets become developed as they do in *Lucifer*, and the carapace loses its posterior spines, although there are three in place of one pair of anterior spines. The telson is distinct from the last abdominal somite, and all the abdominal somites have projecting spines.

The eye-stalks are much longer than they are in the other two forms. The first antenna has a secondary flagellum, as in *Acetes*, and the scale and flagellum of the second antenna are well developed.

The exopodites of the maxillipeds and pereiopods are very long, many-jointed, except in the first maxilliped, and they are longer than the endopodites in all the pereiopods.

The fifth pair of pereiopods are present and like the others. The swimmerets are very long and slender, and the telson very short and forked.

This stage, like the corresponding stage of *Lucifer*, and unlike that of *Acetes*, persists for more than one moult, and the five pleopods make their appearance

together, as rudimentary buds, before the exopodites of the pereiopods and maxillipeds disappear.

The third column of Table VI. shows the resemblances to *Lucifer* and *Acetes* at this stage.

In the immature or *Mastigopus* stage (see Claus's 'Ueber einige Schizopoden und niedere Malacostraken, Messinas') the three forms are almost exactly alike, except as far as the generic distinctions are concerned, and the young *Sergestes* scarcely differs from the young *Lucifer* except in the absence of a neck, the length of the flagellum of the second antenna, and the presence of rudiments of the fourth and fifth pairs of pereiopods.

Comparing the whole course of development of the three forms, as far as it is known, we notice that while the larval stages of *Sergestes* are much more different than those of *Acetes* from the corresponding stages of *Lucifer*, the character of the change at each moult is much more like what we have in *Lucifer* than what we have in *Acetes*.

We cannot fail to notice, in the second place, that the attempt to express the facts of the metamorphosis of these forms, so far as we know them, in a tree-like diagram, would result in a tree placed upside down, with the branches which represent the three Protozoëas much more divergent than those which represent the three young Sergestids. A similarity of type runs through the whole metamorphosis, but it is no more marked at the early stages than it is in the late stages, while the secondary differences are much more conspicuous during the *Zoëa* and *Acanthosoma* stages than they are as we approach the adult form.

While this is true it is also true that if we imagine a metamorphosis which shall agree with these three in all their common features, but shall have none of the features which they do not all share, we shall have something much more like the metamorphosis of *Lucifer* than that of *Acetes* or *Sergestes*, and we must therefore regard the life-histories of these three forms as somewhat divergent modifications of a form of development which is at present more closely adhered to by *Lucifer* than by the other two, and in this metamorphosis we must recognise a *Protozoëa* stage when the two pairs of antennæ are locomotor, the ocellus present, the labrum furnished with a spine, the carapace armed with posterior dorsal and lateral spines and a rostrum; the two pairs of maxillæ, and two pairs of maxillipeds present, and the thoracic and abdominal segments without appendages. This stage persists, with slight modification, through several moults in all of them, and is followed by an *Acanthosoma* stage, in which the carapace has a rostrum and antero-lateral spines, and a smooth posterior edge; the eyes are stalked; the two pairs of antennæ have their adult character; there are at least four pairs of pereiopods with swimming exopodites; the swimmerets are large and have their adult form, and the other abdominal appendages are absent. The duration of this stage and the mode of transition to the next varies in the three forms, but it is followed in all by what may be called a *Mastigopus* stage, characterised by the general features of the family.

In all three forms the somites, and with the exception of the swimmerets the appendages also, develop in serial order from in front backwards.

The interesting question whether we are to attribute to this typical form of development a fifth thoracic somite and appendages must, I think, be left in doubt. A comparison of the Sergestid larvæ seems to indicate its absence, but wider comparison with *Penæus* and the Schizopods seems to lead to the opposite view.

### *Comparison of* Penæus *with the Sergestidæ.*

In order to render the comparative tables as complete as possible, I have added columns showing the corresponding stages of *Penæus* and *Euphausia*.

Fritz Müller has described a number of stages in the development of a species of *Penæus* ("Verwandlung der Garneelen," Arch. f. Naturgeschichte, 1863, pp. 8–23, taf. ii.). The series commences with a *Nauplius* which may belong to the same species, although we have no certainty of this. In a second paper ("Ueber die Naupliusbrut der Garneelen," Zeit. f. Wiss. Zool., xxx., 163–166) he gives, in reply to doubts which had been expressed to him by Spence Bate, Alex. Agassiz, Paul Mayer, and others, the following reasons for believing in the specific identity of all the forms in his series:—1st, the peculiar mode of locomotion; 2nd, the resemblance in colour; 3rd, the great length of both pairs of antennæ; 4th, the character of the mandible; 5th, the presence of four pairs of buds in the *Nauplius*, and four corresponding pairs of limbs in the *Zoëa;* 6th, the similarity in the structure of the heart, digestive tract, and liver in the *Nauplius* and the youngest *Zoëa;* 7th, the presence of frontal organs in both stages. As all the points except the colour would apply to any Crustacean which passes through a *Protozoëa* stage, there is certainly nothing more than a presumption that the whole of his series represents a single species; but as there is no doubt that the *Nauplius* belongs to *Penæus* or to some closely-related form, I have included it in the table.

Fr. Müller's account of the later stages is supplemented by a few additional observations of other species by Claus ("Untersuchungen," &c., pp. 11 and 41, taf. ii. and iii.), and I have compiled the columns in the tables from both sources.

The first *Nauplius* stage (Table II., column 3) appears to be more simple than that of *Lucifer*, as Müller failed to observe any buds to represent appendages posterior to the mandibles.

The *Nauplius* stage is followed by a meta-*Nauplius* stage (Table III., column 2), which is distinguished from that of *Lucifer* by the great size of the blade of the mandible, by the presence of frontal organs, and by the shortness of the carapace.

The next stage is a *Protozoëa* (Table IV., column 5), with a rounded carapace without spines or rostrum, four basal rings and six terminal joints in the endopodite of the second antenna, a spine on the labrum, two pairs of maxillæ, two pairs of maxillipeds, and a long hind body which, according to Claus, is divided into six

thoracic and five abdominal somites, and terminates in a deeply-forked telson with seven pairs of spines.

This stage persists with slight change for several moults, and at the last the buds for the thoracic limbs and swimmerets appear. According to CLAUS, the rudiments of all the abdominal appendages can be seen at an earlier stage.

The passage from the last of the *Protozoëa* series to the first Schizopod stage is attended by a complete change in the structure of the antennæ, and these now assume the adult form. The carapace also acquires two antero-lateral spines and two more at the base of the rostrum. At this time it is much like *Lucifer*, as shown in column 4 of Table VI., but the endopodites of the third pair of maxillipeds and of the pereiopods are rudimentary, and shorter than the very long-jointed exopodites.

The significance of the various stages in the metamorphosis of the higher Crustacea is one of the most interesting questions in the whole field of morphological science, and it has given rise to at least its due share of speculation, but it will not be out of place to examine the relation between the facts which have been described and the various theoretical views which have been expressed upon the subject. In the case of the Sergestidæ it is obvious, in the first place, that the adult *Lucifer* and *Acetes* also, if *Acetes* be an adult, are little more than mature representations of the *Mastigopus* stage, complicated in the case of *Lucifer* by the formation of a neck, and in the case of *Acetes* by the presence of gills, and chelæ on the pereiopods. There can also be little doubt that the Schizopod stage of development in the Sergestidæ and *Penæus* bears a similar relation to the adult Schizopods, especially to *Amphion*, the adult character of which seems to be established by WILLEMÖES-SUHM'S observations (Proc. Roy. Soc., Dec. 9, 1875).

The significance of the *Zoëa* stage in the higher Decapods is one of the most vexed points in Crustacean morphology. We have shown that in the Sergestidæ and in *Penæus* the so-called *Zoëa* stage is nothing but a preparation in the *Protozoëa* for the next or Schizopod stage; that it involves no changes of structure except those which are related to the form which it is to assume after the next moult, and that the *Zoëa*, as a distinct stage, is absent. The life-history of these forms would therefore lead us to suspect that the Brachyuran *Zoëa* is a secondary modification of the more primitive *Protozoëa*, and we may perhaps see in the larval skin which many Crab-*Zoëas* shed soon after or even before they leave the egg, and which usually has a conspicuously forked and very spiny telson—a remnant of the unmodified *Protozoëa* stage.

DOHRN ('Geschichte des Krebsstammes, Jenaische Zeitschr.,' 1871) and FRITZ MÜLLER ('Für Darwin') have held that the typical *Zoëa*, with segmented abdomen and suppressed thorax, is the ontogenetic recapitulation of an ancestral form which has formerly existed as an adult, and DOHRN even goes so far as to recognise the still more remote ancestor of this *Zoëa* type in an embryo ("Untersuchungen über Bau und Entwickelung der Arthropoden; eine neue *Nauplius*-form: Archizœa gigas," Zeit. f. Wiss. Zool., xx., 597), which WILLEMÖES-SUHM has recently shown ("On the

Development of *Lepas fascicularis* and the '*Archizœa*' of Cirripedia," by R. von Willemöes-Suhm, Ph.D., Proc. Roy. Soc., Dec. 9, 1875, pp. 129–130) to be the *Nauplius* of a Barnacle, in all probability *Lepas australis*.

Claus, on the other hand, believes that the *Zoëa* has no such ancestral significance ("Untersuchungen," &c., p. 31). That it has been formed by secondary modification of the *Protozoëa*, and that the views of Müller and others, that the *Zoëa* presents a picture of the remote ancestor of the Malacostraca, is fundamentally erroneous; and not only this, but that the *Protozoëa* itself is the result of the extreme secondary modification of an ancestral form which Claus proposes to call an Urophyllopod, and which he believes to have had the following characteristics ("Untersuchungen," p. 23): A greatly developed shield-like carapace, produced by a fold of the integument in the region of the maxillæ, and probably armed with median and unpaired spines; two maxillary segments and appendages, eight somites of the mid-body with appendages, and six abdominal somites with swimmerets and telson; a many-chambered heart; compound eyes, probably stalked; a first antenna with sensory hairs; locomotor second antennæ, in which the exopodite was probably a scale; the mandible probably lacked a palpus; the metastoma was represented by a pair of paragnathi; the maxillæ had their basal joints modified for mastication, their endopodites reduced to a jointed palp, and the exopodite modified to form a scoop or scaphognathite for regulating the flow of the respiratory current under the carapace.

The following eight pairs of appendages were more like Schizopod feet, and each of them carried a basal gill-plate; the six pairs of abdominal appendages had large basal joints with two branches and gill-plates.

Claus believes that we may recognise in *Nebalia*, which has stalked eyes, a scale on the first antenna; only one long flagellum on the second antenna; a mandibular palp; a highly specialised, long jointed endopodite on the first maxilla; two long limb-like rami on the second maxilla; eight pairs of phyllopod-like thoracic limbs with jointed endopodite, flat, spiny exopodite and gill; six pairs of pleopods, the last two rudimentary; and a seventh somite between the sixth abdominal somite and the deeply-forked telson ("Ueber den Bau und die Systematische Stellung von Nebalia," Zeit. f. Wiss. Zool., xxii. p. 323–330), a very slight modification of this ancestral Urophyllopod.

He gives on pages 69–71 of his "Untersuchungen," &c., a long, minute, and extremely ingenious explanation of the way in which this Urophyllopod stage of development became converted by secondary modification into the Malacostracan *Protozoëa*, and afterwards, by still greater modification in the same direction, into the typical *Zoëa* of the higher Decapods.

The facts which have been detailed and tabulated with reference to the metamorphosis of the Sergestidæ and *Penæus* seem to substantiate at least a portion of this view, and to show that the typical *Zoëa* is a secondary modification of the *Protozoëa*;

but a comparison of these forms with the metamorphosis of *Euphausia*, upon which CLAUS lays especial emphasis, seems to demand a directly opposite interpretation.

If the *Zoëa* has been produced by a secondary modification of the *Protozoëa* we should expect to find the characteristics of the *Protozoëa* better preserved in the Schizopods than in the lower Decapods, and if we find in the Schizopods certain features of the typical *Zoëa*, which are absent in the *Protozoëa* of the lower Macroura, we can hardly accept without question the interpretation which sees, in secondary modification of the latter, the origin of the *Zoëa*. In *Euphausia* the somites appear in regular succession, from in front backwards, but the somites of the abdomen acquire appendages before the pereiopods appear, and there is a stage when the abdomen is fully developed and the thorax almost absent; a stage which, therefore, resembles the Brachyuran *Zoëa* more perfectly than any stage in the development of *Lucifer*, *Acetes*, *Sergestes*, or *Penæus*.

We have no complete history of any one species of *Euphausia*, but the observations of METSCHNICKOFF (Zeit. f. Wiss. Zool., xix., pp. 479–481, and xxi., pp. 390–401), and CLAUS (Zeit. f. Wiss. Zool., xiii., pp. 442–454, and "Untersuchungen," &c., pp. 9 and 33) give us a tolerably complete account of the metamorphosis of the genus.

METSCHNICKOFF'S larva is extremely like that of *Lucifer*, although there are many differences. It is interesting to note that it leaves the egg in a much more rudimentary form, passes through a greater number of moults, and attains to much greater structural complexity than *Lucifer* during the *Nauplius* stage. We can select three stages which agree pretty closely with the egg *Nauplius*, the first free *Nauplius* and the last, or meta-*Nauplius*, of *Lucifer*, but between, after, and before these stages there are others which are not found in *Lucifer*.

The youngest *Nauplius* (Zeit. Zool. xxi., fig. 2) is so much less advanced than the egg *Nauplius* of *Lucifer* six hours before hatching, that it does not seem probable that it normally leaves the egg in this condition.

It has an oval body, without ocellus, mouth, or labrum, and there is no trace of more than three pairs of appendages or of the carapace. At the next stage the swimming hairs of the first three pairs of appendages are fully developed, and the anus, notch, and two spines of the telson are present. In these respects it is more advanced, but in the rudimentary condition of the labrum and metastoma less advanced, than the first free *Nauplius* of *Lucifer*. The buds for the first and second maxillæ and the first pair of maxillipeds are present, but continuous across the median line of the body. According to METSCHNICKOFF, the larva shown in fig. 3 of his first paper is in the next stage of development; but I can scarcely believe that it belongs to the same species, for the ocellus is absent, and the hairs on the three pairs of locomotor appendages are much more rudimentary than they are in fig. 3 of the second pupa.

The next stage (fig. 4) of the second paper agrees with the first free *Nauplius* of

*Lucifer*, so far as the form and number of the appendages is concerned; but the last pair of buds are biramous, and the carapace and telson are well developed. The next stage (fig. 5) of the second paper is more advanced in nearly every respect than the second free *Nauplius* or meta-*Nauplius* of *Lucifer*. The mandible is rudimentary, but still bilobed, with no trace of a blade. The outline of the carapace is free from the body, and its anterior and posterior edges are spiny. It has frontal organs, and the basal joint of the second antenna carries five recurved hooks.

According to the author, figs. 2 and 3 of the first paper show the next stage; but the structure of the hairs on the antennæ, the fact that they are plumose, and the very deep notch in the telson, seem to indicate that this is another species. However this may be, the structural complexity at this and the next (first paper, fig. 6) stage is much greater than we find it in *Lucifer* at the end of the *Nauplius* series.

It will be observed that, while METSCHNICKOFF's larva and the *Nauplius* of *Lucifer* are essentially alike, there is at no time an actual agreement, since certain structures, as the carapace, become developed earlier, and others, as the labrum, later than they do in *Lucifer;* and certain structures, as the frontal organs and the hairs on the base of the antennæ, are entirely absent in *Lucifer*.

In column 4 of Table II. I have compared fig. 4 of METSCHNICKOFF's second paper with the first free *Nauplius* of *Lucifer*, and in column 3 of Table III. his fig. 5 with the last *Nauplius* stage of *Lucifer*.

The various *Protozoëa* stages are shown by CLAUS in plate 1 of the "Untersuchungen," &c. The early *Protozoëa* (Table IV., column 5) is much like that of *Lucifer*, but the carapace is serrated, there is only one pair of maxillipeds, and, according to CLAUS there is a fifth thoracic somite. In the last *Zoëa* stage (Table V., column 5) all the abdominal somites and the rudimentary swimmerets are present, but there is no trace of the second and third pairs of maxillipeds or of the pereiopods.

Up to this point the course of development has followed essentially the same line as in the *Sergestidæ*, but, as we should expect, the *Protozoëa* series is not followed by a larval Schizopod stage, but by a series of moults during which the adult characteristics are gradually acquired. In the loss of the posterior spine of the carapace, the acquisition of antero-lateral spines, and the change in the antennæ from the *Nauplius* form to the adult form, the moult is like that of *Penæus* and the Sergestidæ; but the second and third maxillipeds and the pereiopods appear one at a time in succession from in front backwards, and the abdominal feet appear before the pereiopods. There is no *Zoëa* stage it is true, but the course of development differs from that of *Penæus* and the Sergestidæ in the very feature in which the larvæ of these forms differ from a typical *Zoëa*—the irregular manner in which the pereiopods appear.

I am therefore unable to give CLAUS's interpretation of the significance of these larvæ unqualified acceptance at present, and feel that our groundwork in this department of knowledge can be made sure only by new observations. Every naturalist who can trace the whole life-history of a single species of any of the genera of lower

Malacostraca by actual moults, will not only help us to a sound and thorough appreciation of the significance of Crustacean embryology, but will also contribute to a better knowledge of the relation between ontogeny and phylogeny in the whole province of biology.

The phylogenetic significance of the *Nauplius* stage of development seems to me to rest upon a much firmer basis, and there are many reasons for believing that this is really an ancestral form. Its occurrence in so many widely-separated groups of Crustacea shows its great antiquity, and if it does not represent the adult form of the ancestral Crustacea, but a later larval form which has been produced by secondary modification of the original course of development, this secondary modification must have taken place very early in the history of the group, at a time when the adult forms were very primitive and unspecialised. A sufficient difference between the habits and surroundings of a young animal and those of the adult to favour secondary modification of the young is much less probable in an early unspecialised form, with simple habits, than it is in later and higher forms; and the older a larval form can be shown to be, the more probable does it become that it at one time existed as an adult.

The great age of the *Nauplius* stage and its definite structure therefore indicate that it is ancestral, and nothing except the supposed necessity for believing that the primitive Crustacean had a great number of somites and appendages seems to oppose this view.

I shall try to show further on that the serial homology shown by the parts of the body of one of the higher Crustacea cannot be fully accounted for by assuming, with Balfour ('Comparative Embryology,' p. 418), that the primitive Crustacean had, in addition to its three pairs of appendages similar to those of existing Nauplii, a long segmented body with simple biramous appendages; and I shall also try to show that this homology can be accounted for without any such supposition, so that the peculiarities which Balfour points out—1st, that the mandibles have the form of biramous swimming feet; 2nd, that the second pair of antennæ are biramous swimming feet; 3rd, that the body shows no traces of segmentation; 4th, that the heart is absent; 5th, that the ocellus is the sole organ of vision—must be allowed their full weight, and must not be opposed by any *à priori* assumption of the theoretical need for a greater number of somites and appendages.

TABLE II.—Comparative Table of the Parts of the Nauplii of *Lucifer*, *Penæus*, *Euphausia*, *Apus*, and *Palæmonetes*.

| | First free *Nauplius* of *Lucifer*, $\frac{8}{1000}$th inch long (Plate 2, fig. 25). | First free *Nauplius* of *Penæus* (MÜLLER, "Verw. der Garneelen," fig. 1). | Free *Nauplius* of *Euphausia* (METSCHNICKOFF, Zeit. Zool., xxi., taf. xxxiv., fig. 4). | Free *Nauplius* of *Apus* (BALFOUR, fig. 208 from CLAUS). | Egg *Nauplius* of *Palæmonetes* (FAXON). |
|---|---|---|---|---|---|
| Compound eyes | Absent | Same | Same | Same | Rudimentary |
| Ocellus | Present | Same | Same | Same | Not observed until later |
| Frontal organ | Absent | Same | Same | Absent | Absent |
| Carapace | Absent | Same | Present | Indicated by fold | Absent |
| First antennæ | Uniramous, unjointed, locomotor | Same | Uniramous, obscurely jointed, as long as second, locomotor | Same, but shorter than second | Rudimentary, uniramous |
| Second antennæ | Biramous, unjointed, locomotor, no blade | Same | Biramous, jointed, locomotor, no blade | Biramous, unjointed, locomotor, has basal hook | Rudimentary, uniramous |
| Labrum | Large, without spine | | Moderately large, no spine | Very large, no spine | Small at this stage, but large a little later |
| Mandible | Biramous, unjointed, no blade | Same | Same | Same | Rudimentary, uniramous |
| Metastoma | Rudimentary | Absent | Rudimentary | Five rudimentary body segments | A long unsegmented body without telson |
| First maxilla | Rudimentary | Absent | Rudimentary | | |
| Second maxilla | Rudimentary | Absent | Rudimentary, with spine | | |
| First maxilliped | Rudimentary | Absent | Rudimentary, bilobed | | |
| Second maxilliped | Absent | Absent | Absent | | |
| Third maxilliped | Absent | Absent | Absent | | |
| First pereiopod | Absent | Absent | Absent | | |
| Second pereiopod | Absent | Absent | Absent | | |
| Third pereiopod | Absent | Absent | Absent | | |
| Fourth pereiopod | Absent | Absent | Absent | | |
| Fifth pereiopod | Absent | Absent | Absent | | |
| First abdominal | Absent | Absent | Absent | | |
| Second abdominal | Absent | Absent | Absent | | |
| Third abdominal | Absent | Absent | Absent | | |
| Fourth abdominal | Absent | Absent | Absent | | |
| Fifth abdominal | Absent | Absent | Absent | | |
| Sixth abdominal | Absent | Absent | Absent | | |
| Telson | Absent | Present, with spines | Well marked, deeply notched, has spines | | |
| Anus | Absent | | Absent | | |

TABLE III.—Comparative table of the parts of the last *Nauplius* or meta-*Nauplius* of *Lucifer*, *Penæus*, *Euphausia*, and *Apus*.

| | Second free *Nauplius* of *Lucifer*, $\frac{9}{1000}$th inch long (Plate 2, fig. 26). | Meta-*Nauplius* of *Penæus* (MÜLLER, Zeit. Zool., xix., fig. 2). | Meta-*Nauplius* of *Euphausia* (METSCHNICKOFF, Zeit. Zool.. xx., taf. xxxiv., fig. 5). | Second free *Nauplius* of *Apus* (BALFOUR, after CLAUS). |
|---|---|---|---|---|
| Compound eyes | Absent | Same | Same | Same |
| Ocellus | Present | Same | Same | Same |
| Frontal organ | Not observed | Same | Present | Same |
| Carapace | Indicated by fold | Well marked | Same, margins toothed | Elongated backwards |
| First antenna | Uniramous, unjointed, locomotor, long, sensory hairs | Same | Same | Same, but shorter than second |
| Second antenna | Biramous, unjointed, locomotor, no blade | Biramous, locomotor | Biramous, locomotor, jointed, five blades | Biramous, locomotor, obscurely jointed, has blade |
| Labrum | Large, no spine | Moderately large | Same | Very large |
| Metastoma | Rudimentary, double ? | ? | Rudimentary | Not mentioned |
| First maxilla | Rudimentary | Same | Same | Same |
| Second maxilla | Rudimentary | Same | Same | A number of rudimentary body segments |
| First maxilliped | Rudimentary | Same | Same | |
| Second maxilliped | Absent ? | Rudimentary ? | Absent | |
| Third maxilliped | Absent | Absent | Absent | |
| Thoracic sornites | Absent | Absent | Absent | |
| Abdominal sornites | Absent | Absent | Absent | |
| Telson | Well marked, not forked, has spine | Deeply forked, with spines | Notched, has spines | Forked, has spines |
| Anus | Present | Present | Present | Present |

TABLE IV.—Comparative table of the parts of the first *Protozoëa* in *Lucifer*, *Acetes* (?), *Sergestes*, *Penæus*, and *Euphausia*.

| | 1. First *Protozoëa* of *Lucifer*, $\frac{20}{1000}$th inch long (Plate 2, fig. 27). | 2. CLAUS's larva ('Untersuchungen,' &c., plate iv., fig. 2). | 3. *Protozoëa* of *Sergestes* (CLAUS, 'Untersuchungen,' &c., plate v., fig. 1). | 4. *Protozoëa* of *Penæus* (MÜLLER, 'Verwandlung,' &c., plate ii., fig. 4). | 5. *Protozoëa* of *Euphausia* (CLAUS, 'Untersuchungen,' &c., plate i., fig. 2) |
|---|---|---|---|---|---|
| Compound eye | Absent | Rudimentary | Stalked | Rudimentary | Absent |
| Ocellus | Present | Same | Same | Same | Same |
| Frontal organ | . . . . . | . . . . . | . . . . . | Present | Same |
| Shell gland | Present after first moult | . . . . . | . . . . . | . . . . . | Present |
| Carapace | $\frac{1}{2}$ length of body, rostrum, posterior, dorsal, and lateral spines | $\frac{3}{4}$ length of body, postero-lateral spines | More than $\frac{1}{2}$ length of body, rostrum, postero-lateral and dorsal spines | $\frac{1}{2}$ length of body, no rostrum or spines, edges smooth | More than $\frac{1}{2}$ length of body, no rostrum or spines, edges serrated |
| First antenna | As long as second, jointed, uniramous, locomotor | Not quite as long as second, many joints | Seven joints | Same as *Lucifer* | Same |
| Second antenna | Biramous, jointed, locomotor, no blade | Same | Same | Same | Same |
| Labrum | Large, small spine | Small, no spine described | Has spine | Same | Same |
| Metastoma | . . . . . | Bilobed | Bilobed | . . . . . | Bilobed |
| Mandible | Blade, no palp | Same | Same | Same | Blade and rudiment of limb |
| First maxilla | Adult form, scaphognathite | Like *Lucifer* | Same | Same | Same |
| Second maxilla | Has scaphognathite | Same | Same | Same | Same |
| First maxilliped | Large, biramous | Same | Same | Same | Same |
| Second maxilliped | Rudimentary, biramous | Same | Large, biramous | Rudimentary, biramous | Somite, no appendage |
| Third maxilliped | Somite, no appendage | A segmented region | Rudimentary | Segment, no appendage | Same |
| First pereiopod | Somite, no appendage | A segmented region | Somite, no appendage | Same | Same |
| Second pereiopod | Somite, no appendage | A segmented region | Somite, no appendage | Same | Same |
| Third pereiopod | Somite, no appendage | A segmented region | Somite, no appendage | Same | Same |
| Fourth pereiopod | Somite, no appendage | A segmented region | Somite, no appendage | Same | Same |
| Fifth pereiopod | No somite | A segmented region | Somite, no appendage | Same | Same |
| Abdominal somites | Represented by long unsegmented region about $\frac{1}{3}$ the length of the body | Same, less than $\frac{1}{4}$ length of body | Same, less than $\frac{1}{3}$ length of body | Same, $\frac{1}{3}$ length of body, six abdominal somites appear, according to CLAUS, before next moult | Same, less than $\frac{1}{3}$ length of body |
| Telson | Notched, four pairs large spines, one pair small ones | Deeply forked, six pairs of spines | Still more forked, with six pairs of spines | Deeply forked, seven pairs of spines | Posterior edge straight, seven pairs of spines |

TABLE V.—Comparative table of the parts of the last *Protozoëa* of *Lucifer*, *Acetes*, *Sergestes*, *Penæus*, and *Euphausia*.

| | Last *Protozoëa* of *Lucifer*, $\frac{59}{1000}$th inch long (Plate 5, fig. 43). | Last *Protozoëa* of *Acetes*, $\frac{67}{1000}$th inch long (fig. 77). | *Elaphocaris* of *Sergestes* (CLAUS, 'Untersuchungen,' taf. vi., fig. 1). | Last *Protozoëa* of *Penæus* (MÜLLER, 'Verwandlung,' &c., fig. 7). | Last *Protozoëa* of *Euphausia* (CLAUS, 'Untersuchungen,' taf. i., fig. 4). |
|---|---|---|---|---|---|
| Compound eye | Rudimentary | Stalked, short. | Stalked, long | Stalked, short | Rudimentary |
| Ocellus | Present | Same | Same | Same | Same |
| Carapace | Dorsal spine, two postero-lateral spines, and rostrum, all simple | Same | Same, all compound | No posterior spines | No rostrum, dorsal spine only |
| First antenna | *Nauplius*-like, two jointed | Same, three jointed | Same, seven jointed | Like *Lucifer*, but with sense hairs | Like *Lucifer* |
| Second antenna | *Nauplius*-like | Same | Same, but without basal rings, no endopodite | Like *Lucifer* | Same |
| Labrum | Has spine | Same | No spine | Has spine | No spine |
| Mandible | Adult form, no palp | Same | Same | Same | Same |
| First maxilla | Two basal joints, jointed endopodite, scaphognathite | Same | Same | Same | Same, without scaphognathite |
| Second maxilla | Has scaphognathite | Same | Same | Same | Same |
| First maxilliped | Biramous, large | Same | Same | Same | Rami very short and simple |
| Second maxilliped | Small, biramous | Same | Large | Large | Somite, without appendages |
| Third maxilliped | Bilobed bud | Same | Small, but functional | Bilobed bud | Somite, without appendages |
| First pereiopod | Somite, rudimentary appendages | Same | Same | Same | Somite, without appendages |
| Second pereiopod | Somite, rudimentary appendages | Same | Same | Same | Somite, without appendages |
| Third pereiopod | Somite, rudimentary appendages | Same | Same | Same | Somite, without appendages |
| Fourth pereiopod | Somite, rudimentary appendages | Same | Same | Same | Somite, without appendages |
| Fifth pereiopod | Somite and appendages absent | Same | Somite, rudimentary appendages | Same | Somite, without appendages |
| First abdominal somite | Somite, no appendages | Same | Same | Same | Same |
| Second abdominal somite | Somite, no appendages | Same | Same | Same | Same |
| Third abdominal somite | Somite, no appendages | Same | Same | Same | Same |
| Fourth abdominal somite | Somite, no appendages | Same | Same | Same | Same |
| Fifth abdominal somite | Somite, no appendages | Same | Same | Same | Same |
| Sixth abdominal somite | Somite united to telson, appendages present as bilobed buds | Same | Same | Same | Same |
| Telson | Notched | Forked | Deeply forked | Same | Straight |

TABLE VI.—Table of the parts of the Schizopod larva of *Lucifer*, *Acetes*, *Sergestes*, and *Penæus* at the first stage.

| | Schizopod stage of *Lucifer* (Plate 6, fig. 50). | *Acanthosoma* stage of *Acetes* (fig. 84). | *Acanthosoma* of *Sergestes* (CLAUS, 'Untersuchungen,' taf. v., fig. 6). | Schizopod stage of *Penæus* (MÜLLER, 'Verwandlung,' &c., taf. 11, fig. 7). |
|---|---|---|---|---|
| Ocellus | Present | Same | | |
| Compound eye | Stalk short | Same | Stalk, very long | Stalk short |
| Carapace | $\frac{1}{3}$ length of body, rostrum, two antero-lateral spines, no posterior spines | Same | $\frac{1}{3}$ length of body, rostrum, six pairs of antero-lateral spines, no posterior spines | $\frac{1}{3}$ length of body, rostrnm, two pairs of antero-lateral spines, no posterior spines |
| First antenna | Plumose fringing hairs, long shaft, one short rudimentary flagellnm | Same, with a second rndimentary flagellum | Same | Same |
| Seeond antenna | Rudimentary at first, but it acquires scale and flagellum at next monlt | Scale and flagellum | Same, flagellnm long | Seale large, flagellum rudimentary |
| Labrum | Has spine | | | No spine |
| Mandible | No palp | | Same | Same |
| First maxilla | Like that of *Protozoëa* | | Same | Same |
| Seeond maxilla | Scaphognathite rudimentary | | Same | Same |
| First maxilliped | Rami equal | | Endopodite longest | Same |
| Seeond maxilliped | Short exopodite, long endopodite, both free and movable | Exopodite alone free and movable | Equal, both free | Biramous |
| Third maxilliped | Short exopodite, long endopodite, both free and movable | Exopodite alone free and movable | Endopodite longest | Biramous |
| First pereiopod | Short exopodite, long endopodite, both free and movable | Exopodite alone free and movable and chelate | Exopodite very long, no ehela | Endopodite rndimentary, exopodite very long, jointed |
| Second pereiopod | Short exopodite, long endopodite, both free and movable | Exopodite alone free and movable and ehelate | Exopodite very long, no ehela | Endopodite rndimentary, exopodite very long, jointed |
| Third pereiopod | Short exopodite, long endopodite, both free and movable | Exopodite alone free and movable and ehelate | Exopodite very long. no ehela | Endopodite rudimentary, exopodite very long, jointed |
| Fourth pereiopod | Short exopodite, long endopodite, both free and movable | Endopodite absent | Exopodite very long, no ehela | Endopodite rudimentary, exopodite very long, jointed |
| Fifth pereiopod | Somite absent | Same | Exopodite very long, no ehela | Endopodite rndimentary, exopodite very long, jointed |
| First abdominal | Somite present, appendages absent | Appendages rudimentary | Like *Lucifer* | Same |
| Seeond abdominal | Somite present, appendages absent | Appendages rudimentary | Like *Lucifer* | Same |
| Third abdominal | Somite present, appendages absent | Appendages rudimentary | Like *Lucifer* | Same |
| Fourth abdominal | Somite present, appendages absent | Same | Same | Same |
| Fifth abdominal | Somite present, appendages absent | Same | Same | Same |
| Sixth abdominal | Like adult | Same | Same | Same |
| Telson | Long, narrow, notehed | Short, wide, notehed | Short, deeply eleft | Very long, forked |

## VII. Serial Homology and Bilateral Symmetry in the Crustacea.

The Phyllopods and the highest Brachyura are connected with each other by a tolerably complete series of intermediate forms, and as we pass this series in review we cannot fail to notice that, as has been so frequently pointed out by morphologists, each successively higher form is a little in advance of the one next below it in the degree to which the functions and structure of the somites and appendages are subordinated to the individuality of the organism as a whole.

In the lower forms the body is made up of a series of nearly similar somites, and the appendages, with the exception of those at the anterior end of the body, are essentially alike in structure and their functions are indentical throughout the series. The greater part of the body of such a Crustacean as *Artemia* consists of a series of similar somites, and in *Apus* we find more than sixty pairs of limbs which agree with each other so perfectly in function as well as in structure that any one of them might be substituted for any other without involving any essential change in the structure of the animal as a whole.

At the other end of the series we have Crabs with the primitive distinctness of the somites so obscured by the centralised individuality of the whole organism that it cannot be traced at all without careful study and comparison of various stages in the life of a number of forms.

Comparing the various appendages of a Crab with each other we find that their functions are not at all alike. The mandibles are nothing but masticating organs, and the power which they once had, and which they still retain in the *Nauplius* of *Lucifer* to aid in locomotion, has entirely disappeared.

Other appendages have become organs for procuring food, or weapons of offence or defence; others have become walking legs; others long oars or paddles; others again have lost all limb-like functions, and are changed into accessory reproductive organs; whilst others again have entirely disappeared.

In accordance with this specialisation of each appendage to a particular function, a corresponding structural change has been brought about, and it is only after careful study of the younger stages that we perceive the mandibles, maxillæ, foot-jaws, walking and swimming legs, and copulatory organs of an adult Crab to be as strictly homologous with each other as are the unspecialised appendages of *Apus*.

The integration of the somites into a centralised whole has been accompanied by a differentiation of each appendage from the others, and a specialisation to a restricted function.

An adult Crab resembles and differs from one of the higher Macroura in about the same way that it resembles and differs from its own *Megalops* larva, and the transition from the larval form to the adult form is accompanied, like the transition from an adult low Crustacean to a high one, by increased dependence of the various parts on each other, by the increased prominence of the general individuality over the indivi-

dualities of the somites or metameres, and by the increased structural and functional specialisation and differentiation of each appendage as compared with the others.

This series of changes is so well exemplified by the study of adult and larval Crustacea; it is so remarkable and interesting; so very conspicuous and unquestionable, that it has long attracted the attention and called forth the speculation of morphologists. It is natural to suppose that the process of change which is open to our observation through study and comparison of living Crustacea, is a continuation of a similar process which went on in the remote past. There seems then at first sight to be reason for believing that, if we could go far enough back, we should find the individuality of the whole organism gradually disappearing and giving place to the separate individualities of the component somites; that we should find the specialisation of the appendages gradually disappearing, until we should at last find, as the remote ancestor of the Crustacea, a series or community of independent organisms, each one essentially like the others, and able to provide for its own wants and to lead an independent existence when accidentally or naturally detached.

This view has been advocated at length by Hæckel ('Generelle Morphologie,' 1866) and by Spencer ('Principles of Biology,' vol. xi., 1867), and used by both these writers as an explanation of the origin of all segmented or compound animals and plants. It has been accepted, with more or less qualification, by many other writers, although Huxley ('Oceanic Hydrozoa') and Metschnickoff (Zeit. f. Wiss. Zool., xxiv.) have pointed out that, even in the Siphonophoræ, where the individualities of the units in the compound are extremely well marked, the view that the organism has been evolved by the gradual integration and specialisation of originally independent Zooids is attended with serious difficulties.

So far as we can see there is no reason why the Crustacea might not have originated in this way, by the gradual integration and differentiation of a community of independent metameres, but the evidence which is attainable seems to directly oppose the belief that this has actually happened. We are able to trace the higher Decapods back, very satisfactorily, to a Phyllopod-like ancestor with a long series of undifferentiated somites and appendages, but even here the somites are simply parts of the body, and they furnish no more evidence than those of a Crab to show that they ever were the independent organisms of a community.

When we attempt to go still further back we find that the facts of embryology, if they show any thing whatever about the phyllogeny of the Crustacea, lead us back to a *Nauplius* with three inter-dependent somites and three pairs of specialised appendages, rather than to a form with a great number of unspecialised somites and similar appendages.

Turning now to a somewhat different aspect of the subject, we notice that, if we confine ourselves to structure, and leave out of sight the question of origin, there is the closest similarity between serial homology and the homology between the corre-

sponding organs of allied animals which OWEN has proposed to distinguish by the term "special homology."

The structural relation between one appendage of *Lucifer*, say the first pereiopod, and another, such as the swimmeret, is identical with the relation between the pereiopod of *Lucifer* and that of *Squilla*, or a Crab or Lobster. In both cases we have a fundamental similarity of plan, which is independent of external conditions; and joined to this essential similarity, we have a more superficial diversity of structure which is plainly due to difference in the functions of the appendages, and their relations to the external world. The resemblance between the two kinds of homology does not stop here. Tracing the ontogeny of the appendages we find that there is much less difference between the larval pereiopods of *Lucifer* and those of the Lobster than there is between the appendages of the adults, and we find exactly the same thing when we compare the pereiopod and swimmeret of the same individual at earlier and earlier stages of development.

There is precisely the same resemblance between symmetry and special homology. The right and left claws of the Common Crab (*Callinectes*) are not exactly alike, since the cutting edge of one claw is sharp and set with pointed teeth, while the edge of the other is thick, with thick blunt crushing tubercles. The two appendages are alike in plan or homologous, but each is fitted for a specialised function by a slight structural peculiarity. In this case, as in the others, the differences are less marked, and the common plan more closely followed, in the larva than in the adult.

Serial homology and bilateral symmetry are thus seen to be like special homology in all purely structural features. In each case the homology is a resemblance which is independent of external conditions, but which may be obscured by secondary modifications whenever external conditions render it necessary.

In each case, too, the secondary modifications become less marked, and the underlying plan more evident as we pass back from the adult to earlier and earlier stages of development. We must therefore include all three kinds of homology in a single class or category, and the employment of one term to denote the phenomena of special homology, of another for serial homologies, and a third for bilateral homologies, and others for other sorts of general homology must not be allowed to obscure the fact that they are all different forms of the same thing, essential similarity joined to superficial diversity. The terminology which has been employed by BRONN, HÆCKEL, LANKESTER, and others for the different kinds of homology is valuable, and the only reason why I have not made use of it is that the more familiar terms, "serial homology" and "bi-lateral symmetry" answer every purpose equally well in treating of the Arthropods. HÆCKEL's subdivisions are natural, but they are simply subdivisions of a great class of similar phenomena, which must still be included under the general term "homology."

Special homology may be defined in two ways, morphologically and phylogenetically. From the morphological point of view an homology is a similarity in essential plan of structure, which may be obscured by differences due to diversity of function. From

the phylogenetic point of view it is a resemblance which is due to community of origin or heredity from a common ancestor, while the differences between homologous organs are due to the divergence of allied forms, and to the selection and perpetuation, through natural selection, of variations which are in accordance with changed conditions of life.

Now are the phenomena of serial and lateral homology like those of special homology in this second or phylogenetic sense, as well as in a morphological sense?

On the assumption that the remote ancestor of the Crustacea was a community of independent organisms, all of which had inherited their organisation from the same parent, we might answer that serial homology is like special homology when viewed from a phylogenetic stand-point, and if we assume that this series was at first double, and that the progress of centralisation suppressed one side of each metamere as the community became gradually fused into a bilateral organism, we may make the same statement regarding symmetry.

A process of evolution of this sort is not impossible, and in some cases there seems to be evidence that it has actually occurred. Pyrosoma is clearly a community of independent Ascidians, which has been brought by natural selection into a form which has a certain degree of individuality of its own, independent of that of the component units; although in this case the peculiar form of the community has called for little differentiation, and the polymorphism is therefore very slight.

The salpa-chain is a bilateral community, and in Doliolum we have a similar community which exhibits considerable polymorphism. If this process were carried a little further we might ultimately have a bilaterally symmetrical organism in which corresponding parts in the series or on opposite sides should be strictly homologous by descent; but we are not therefore justified in assuming that all instances of serial and lateral homology have originated in this way, and even if we were a more careful analysis will show that the assumption does not remove all the difficulties.

If we grant, for the sake of argument, that the Crustacea are not the descendants of a *Nauplius*, but of a remote ancestor which consisted of a community of independent metameres, we shall still be forced to recognise a bond of relationship between the limbs of a Decapod, which is very much more recent than that which they owe to common descent from the parent of the group of Zooids which formed the ancestral community.

A reference to the figures will show that the first, second, and third thoracic limbs of the adult *Lucifer* agree with each other, or are homologous, in certain features which are not present in a Schizopod. The exopodite is absent and the endopodite is long and slender in all of them, and it carries short hairs along its entire length, while, in the Schizopod-larva, the exopodite is present, and the long hairs are restricted to the tip of the stout endopodite. We must therefore recognise a bond of union or homology between these three appendages which has determined that they shall be like each other in the adult *Lucifer*, and the assumption that this similarity is due to heredity from the parent of the imaginary metameres which joined together to form

the primitive Crustacean is out of the question, for we know that no further back than the Schizopods these appendages had quite a different structure.

The study of serial or lateral homology in other groups of animals forces us to the same conclusion, and compels us to recognise a persistent bond of union between them which cannot be due to what we usually understand by heredity.

On the assumption that the Vertebrates are the descendants of a community of metameres, the genetic relationship between a man's arm and a bird's wing must be almost infinitely closer than that between a man's arm and his leg, and this again much more recent than that between his right and his left arm. The arm and wing inherit their homology from the anterior limb of the common ancestor of man and the birds, but man's arm and leg have no common ancestor more recent than the limb of the parent of the imaginary metameres which gave origin, by their union, to the ancestor of the Vertebrates, and the common ancestor of the right and left arms must have been still more remote.

When we compare man's arm and leg we find that they have homologous features which are not only more recent than the time when man's ancestors diverged from the ancestors of the birds, but more recent than the separation of the anthropoid and simian stems. They resemble each other in the texture of the skin and in the shape of the nails, and these resemblances are strictly homological, that is, they are not due to external conditions, but in spite of them; and we meet with countless similar resemblances all through the animal kingdom. They are not accounted for by the "metamere" theory, even if this is fully accepted, for in many cases they are not old, but are of recent acquisition.

In the case of the Crustacea the assumption that the remote ancestor of the group had a many-jointed body does not account for them; and as the supposed necessity for an explanation of serial homology is the only reason for believing that this remote ancestor had a great number of body-segments, it is clearly illogical to reject the embryological evidence that this ancestor was a three-jointed *Nauplius*, in order to hold an hypothesis which fails to account for the facts which are supposed to render it necessary.

## Explanation of the Plates.

All the figures where the magnifying power is not stated were drawn with a power of 160 diameters (Zeiss, Oc. 1, Obj. D); but the actual amplification of the drawings is not uniform. In copying the original sketches it has been convenient to reduce the size of some of them, and no inference as to relative size should be drawn from any of them except where measurements are given.

In order to render the figures as truthful and lifelike as possible, the animals were subjected to very little confinement while under examination, and as their incessant

and violent movements rendered the use of a camera impossible, they are not drawn to a fixed scale.

In all the Plates the capital reference letters are used to denote the same parts, as follows :—

*A.* First antenna.
*A.* 1 to *A.* 6. The series of abdominal somites.
*An.* Second antenna.
*C.* Carapace.
*E.* Compound eye.
*L.* Labrum.
*M.* Mandible.
*Mp.* 1, *Mp.* 2, *Mp.* 3. The first, second, and third maxillipeds.
*Mx.* 1, *Mx.* 2. The first and second maxillæ.
*Oc.* Ocellus.
*Pl.* 1–*Pl.* 6. The six pairs of abdominal appendages.
*Pr.* 1–*Pr.* 4. The four pairs of thoracic limbs.
*R.* Rostrum.
*T.* 1–*T.* 4. The four thoracic somites.
*T.* Telson. (*Tl.* in Plate 3, fig. 26.)

## PLATE 1.

The letter *a* in figs. 1 to 8, which were all drawn from the same egg, marks the same point in all.

Fig. 1. An egg during the period of rest which follows the first period of segmenting activity.

Fig. 2. The same egg at the beginning of the second period of segmenting activity, five minutes after the stage shown in fig. 1.

Fig. 3. The same egg five minutes later. One of the primary segments is beginning to divide into two.

Fig. 4. The same egg ten minutes later. One of the primary spherules is perfectly divided into two, and the division of the other is less advanced.

Fig. 5. The same egg five minutes later, and completely divided into four equal segments. This stage ends the second period of segmenting activity.

Fig. 6. The same egg, fifteen minutes later, during the second period of rest.

Fig. 7. The same egg, ten minutes later, entering upon the third period of activity.

Fig. 8. The same egg, twenty-five minutes later, divided into eight equal spherules. This stage ends the third period of activity.

Fig. 9. Another egg during the third period of rest.

Fig. 10. Another egg near the end of the fourth period of activity, and divided into sixteen equal spherules, arranged around a central segmentation cavity.

Fig. 11. Optical section along the principal axis of a somewhat older egg, showing the yolk spherule, *c*, and the segmentation cavity, *b*.

Fig. 12. Optical section of the same egg at right angles to the one shown in fig. 11.

*b*. The segmentation cavity.

*c*. The yolk spherule.

## PLATE 2.

Fig. 13. An optical section of an egg somewhat older than the one shown in fig. 11.

Fig. 14. Optical section at right angles to that of fig. 13.

Fig. 15. Optical section of an egg a little older than the one shown in fig. 13.

*d*. Orifice of invagination.

Fig. 16. Optical section of a still older egg in the same position as figure 15.

Fig. 17. Optical section of a still older egg in the same position.

Fig. 18. Surface view of the formative pole of the egg shown in fig. 17.

Fig. 19. Optical section along the principal axis of a still older egg.

Fig. 20. A similar section of a still older egg.

Fig. 21. Ventral view of an embryo in the egg-shell 24 hours after oviposition.

*e*. Anterior end of body.

*f*. Large spherules in the region of the digestive tract.

*g*. Metastoma.

Fig. 22. Dorsal view of the same embryo.

(*e* and *f* as in fig. 21.)

*h*. Cerebral ganglia.

*i*. Pigment spots.

*m*. Muscles.

Fig. 23. Similar aspect of the same embryo artificially removed from the egg shell. (Letters as in fig. 22.)

## PLATE 3.

Fig. 24. Ventral view of the same embryo, seen from a point of view a little anterior to that of fig. 21.

*ex*. Exopodite.

*en*. Endopodite.

(The other letters as in fig. 21.)

Fig. 25. Side view of the *Nauplius*, $\frac{8}{1000}$th inch long, as it leaves the egg 36 hours after oviposition.

*g*. Metastoma.

*p*. Pigment spots.

*ex*. Exopodite.

*en*. Endopodite.

Fig. 26. Side view of a *Nauplius*, $\frac{9}{1000}$th inch long, and a little older than the one shown in fig. 25. The animal is a little flattened by pressure. In a ventral view of the same larva the anus was visible at the point marked *a.* in the figure.

*œ.* Œsophagus.
*s.* Stomach.
*l.* Large cells around stomach.
*i.* Intestine.
*ga.* Cerebral ganglia.
*n.* Ventral nerve-chain.
*p.* Pigment spots.

Fig. 27. Dorsal view of a *Protozoëa*, $\frac{20}{1000}$th inch long, which moulted from the *Nauplius* shown in fig. 26, about 96 hours after oviposition.

*ga.* Cerebral ganglia.
*s.* Stomach.
*h.* Heart.
*i.* Intestine.
*p.* Pigment spots.
*a.* Anus.
*m.* Muscles of œsophagus.
*ls.* Postero-lateral spines of carapace.
*ds.* Posterior dorsal spine of carapace.
*abd.* Unsegmented portion of abdomen.
*ex.* Exopodite.
*en.* Endopodite.

Fig. 28. Right mandible of the same specimen seen from below.

Fig. 29. Right mandible seen from behind.

Fig. 30. Back or outer surface of first maxilla of the same specimen.

*sc.* Scaphognathite.

Fig. 31. Posterior surface of left-second maxilla of the same specimen.

*sc.* Scaphognathite.
*b.* Basal joint.
*en.* Endopodite.

Fig. 32. Left-first maxilliped of the same specimen; posterior surface.

*ex.* Exopodite.
*en.* Endopodite.
*b.* Basal joint.

Fig. 33. Right-second maxilliped of the same specimen.

*ex.* Exopodite.
*en.* Endopodite.
*b.* Basal joint.

Fig. 34. A *Protozoëa*, $\frac{27}{1000}$th inch long, and a little older than the one shown in fig. 27.

*œ.* Œsophagus.

*pp.* Anul pigment spots.

(Other letters as in fig. 27.)

## PLATE 4.

Fig. 35. Side view of another larva at the stage shown in fig. 34.

*ga.* Cerebral ganglia.

*s.* Stomach.

*sg.* Shell gland.

*h.* Heart.

Fig. 35A. Surface view of the area of attachment of the œsophageal muscles of the same larva.

Fig. 36. Second antenna of the same specimen.

*b.* Basal joint.

*ex.* Exopodite.

*en.* Endopodite.

Fig. 37. Mandible, at same stage, seen from below.

Fig. 38. First maxilla of left side at same stage.

1 and 2. The two cutting joints of the basal portion.

*ex.* Exopodite.

*en.* Endopodite.

Fig. 39. Left-second maxilla at same stage.

*b.* Basal portion.

*en.* Endopodite.

*sc.* Scaphognathite.

Fig. 40. Left-first maxilliped at same stage.

*ex.* Exopodite.

*en.* Endopodite.

Fig. 41. Left-second maxilliped at same stage.

*ex.* Exopodite.

*en.* Endopodite.

Fig. 42. Ventral view of the same larva after the next moult and $\frac{35}{1000}$th inch long.

Fig. 42A. Outline of the anterior end of fig. 42, more enlarged.

*b.* Basal joints of appendages.

*ex.* Exopodites.

*en.* Endopodites.

*sc.* Scaphognathite.

## PLATE 5.

Fig. 43. Ventral view of the last *Protozoëa* (Dana's *Erichthina demissa*), $\frac{50}{1000}$th inch long.

*ex.* Exopodite of second antenna.

*en.* Endopodite of second antenna.

Fig. 44. Dorsal view of the same larva (Zeiss, A. 2).

*ds.* Median dorsal spine of carapace.

*ls.* Postero-lateral spines of carapace.

Fig. 45. Side view of the same larva at the same stage.

*ds.* Median dorsal spine of carapace.

*tg.* Thoracic ganglia.

*i.* Intestine.

Fig. 46. Posterior surface of left first maxilla of the same larva.

1 and 2. Cutting joints of basal portion.

*en.* Endopodite.

*sc.* Scaphognathite.

Fig. 47. Left second maxilla of the same larva.

*b.* Basal joint.

*sc.* Scaphognathite.

*en.* Endopodite.

Fig 48. Left first maxilliped of same larva.

*b.* Basal joint.

*ex* Exopodite.

*en.* Endopodite.

Fig. 49. Left second maxilliped of same larva.

(Letters as in fig. 48.)

## PLATE 6.

Fig. 50. First Schizopod stage (this stage is the equivalent of Dana's genus *Sceletina;* of Claus's *Acanthosoma* stage; and of Willemöes-Suhm's *Amphion* stage). The larva passes, by a single moult, which was frequently observed in isolated specimens, from the stage shown in fig. 43 to the one which is shown in this figure.

Fig. 51. Mandible at same stage.

Fig. 52. First maxilla at same stage.

Fig. 53. Second maxilla at same stage.

Fig. 54. *Sceletina* larva, two moults later (Zeiss, A. 2).

*s.* Antero-lateral spine.

*p.* Pigment spot on fourth abdominal somite.

Fig. 54A. Outline of anterior end of carapace.
Fig. 55. Dorsal view of the anterior end of the same larva.
Fig. 56. First antenna of the same larva.
Fig. 57. Second antenna of the same larva.
Fig. 58. Mandible at same stage.
Fig. 59. Locomotor appendages of the left side, at same stage, seen from above.

## PLATE 7.

Fig. 60. Side view of a young *Lucifer*, about $\frac{25}{100}$th inch long, which was produced by the moulting of a larva like that shown in fig. 54 (this stage agrees pretty exactly with the *Mastigopus* stage of *Sergestes*).
*g.* Antennal gland.
*n.* "Neck."
*c.* Carapace.
Fig. 61. Half-grown *Lucifer*, about $\frac{1}{2}$ an inch long.
*g.* Antennal gland.
*cg.* Cerebral ganglia.
*co.* Commissures to ventral ganglia.
*s.* Cephalic pouch of stomach.
*h.* Heart.
*c.* Carapace.
Fig. 62. Inner surface of mandible of adult.
Fig. 63. Outer surface of mandible of adult.
Fig. 64. Outer surface of first maxilla of adult.
Fig. 65. Inner surface of same.

## PLATE 8.

Fig. 66. Head of a small female about $\frac{2}{3}$rds of an inch long, seen from below.
Fig. 67. Second maxilla of same.
Fig. 68. First maxilliped of right side of adult.
Fig. 69. Inner surface of same.
Fig. 70. Second maxilliped of adult.

## PLATE 9.

Fig. 71. Dorsal view of tip of telson of adult female.
Fig. 72. Side view of last abdominal somite and swimmerets of adult female.
Fig. 73. The same parts of an adult male.

Fig. 74. Side view of posterior half of carapace and first abdominal somite of a mature female, to show the reproductive organs. In order to reduce the number of figures this specimen is represented with its ovaries full of ripe eggs, while a large bunch of developing eggs are attached to the basal joints of the last pair of thoracic appendages, but these two features are never exhibited completely at the same time in a single individual.

*ca.* Carapace.
*h.* Heart.
*i.* Intestine.
*tg.* Thoracic ganglia.
*ov.* Ovary.
*od.* Oviduct.
*sr.* Seminal receptacle.

Fig. 75. The corresponding part of the body of an adult male.

*c.* Carapace.
*h.* Heart.
*i.* Intestine.
*tg.* Thoracic ganglia.
*a.* First abdominal somite.
*t.* Testis.
*vd.* First division of vas deferens.
*sp.* Second division.
*sr.* Third division.

Fig. 76. First pleopod of young male.

Fig. 78. Side view of the larva shown in Plate 10, fig. 77 (Zeiss, A. 2).

Fig. 79. Dorsal view of the same larva.

Fig. 80. Mandible of the same larva.

Fig. 81. First maxilla of the same larva.

*en.* Endopodite.
*sc.* Scaphognathite.

Fig. 82. Second maxilla of the same larva.

*sc.* Scaphognathite.
*en.* Endopodite.

## PLATE 10.

Fig. 77. Ventral view of the last *Protozoëa* stage of *Acetes* $\frac{67}{1000}$th inch long.

*ex.* Exopodite of second antenna.
*en.* Endopodite of second antenna.

Fig. 85. The specimen shown in fig. 84, after another moult and $\frac{80}{1000}$th inch long.

Fig. 86. First antenna of the same larva.

Fig. 87. Second antenna of the same larva.

## PLATE 11.

Fig. 84. Ventral view of the specimen shown in fig. 81, after the next moult and $\frac{70}{1000}$th inch long.

*ex.* Exopodite.

*en.* Endopodite.

Fig. 83. First maxilliped of the larva shown in Plate 10, fig. 77.

Fig. 88. Second and third maxillipeds and periopods of the larva shown in Plate 10, fig. 85.

Fig. 89. First pleopod of same larva.

Fig. 90. An older specimen $\frac{15}{100}$th inch long, which was captured at the surface.



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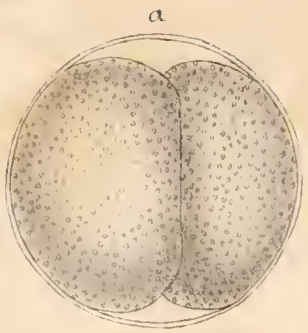


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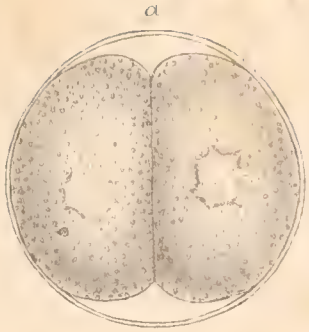



Fig. 2

Fig 3

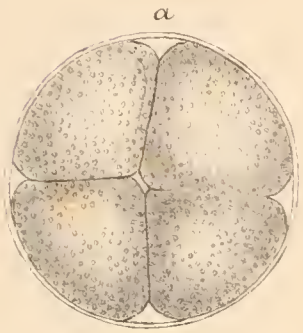
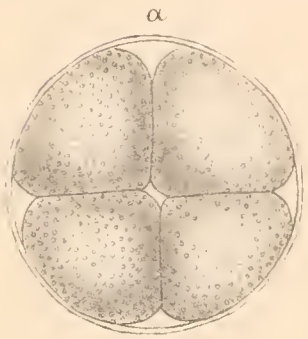



Fig 4

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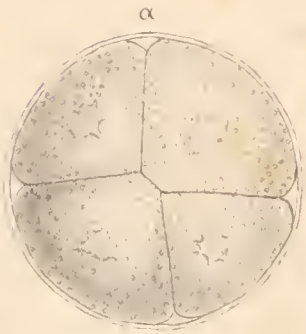


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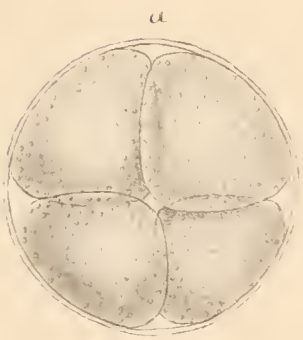


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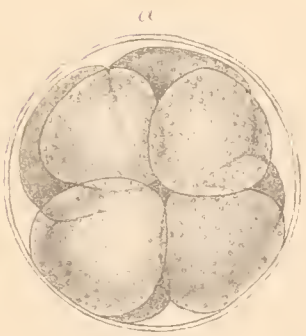
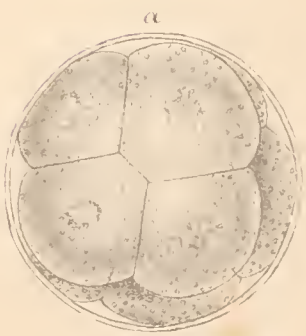



Fig. 8

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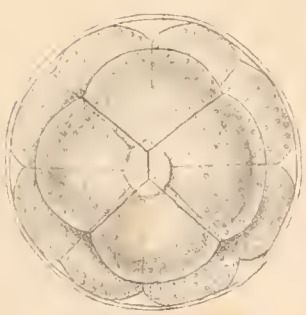

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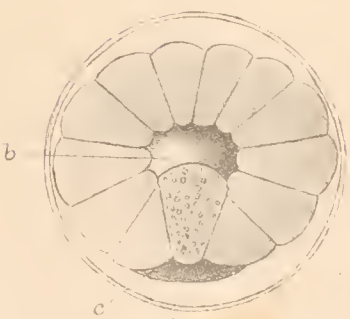


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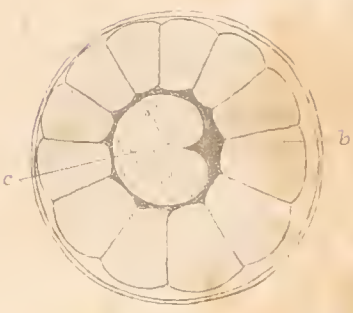
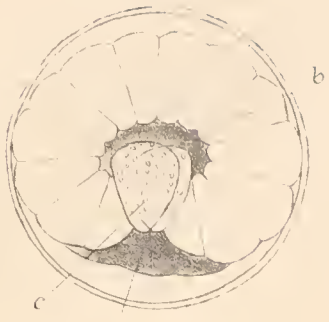



Fig 12

W. K. B. ad nat. del.

Wes. Newman & Co. lith.



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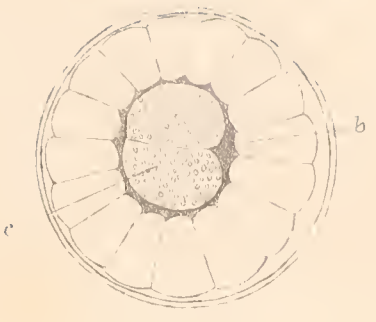
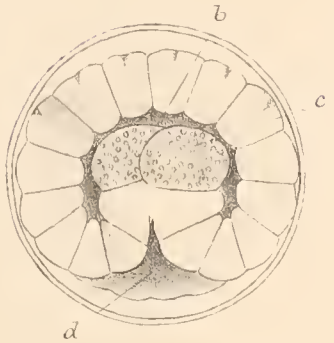


Fig. 14.

Fig. 15.



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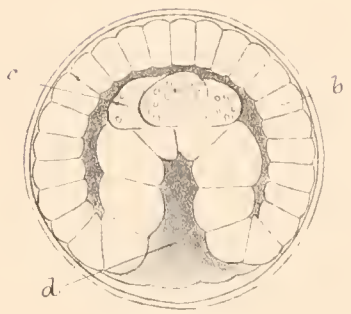
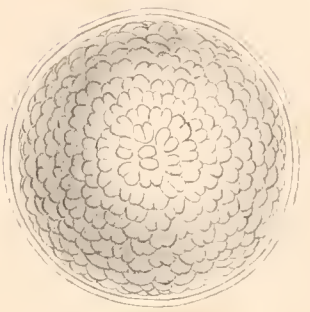


Fig 17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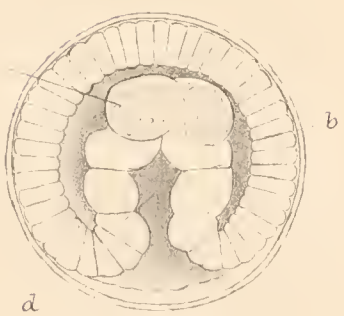
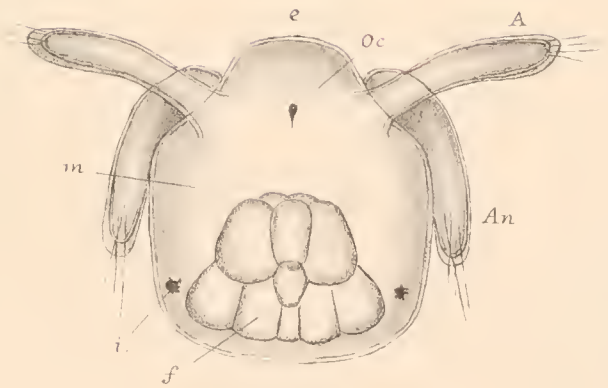


Fig 18.

Fig. 20



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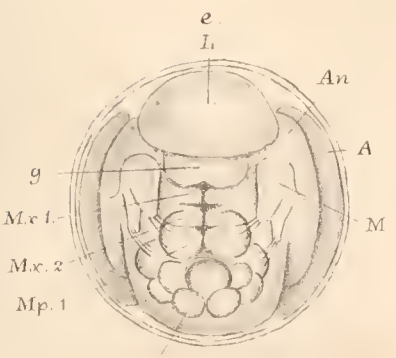

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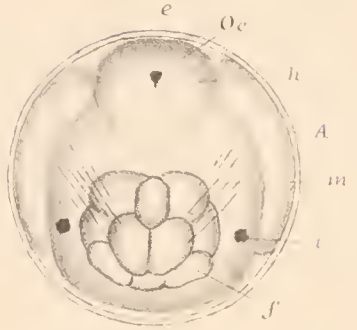

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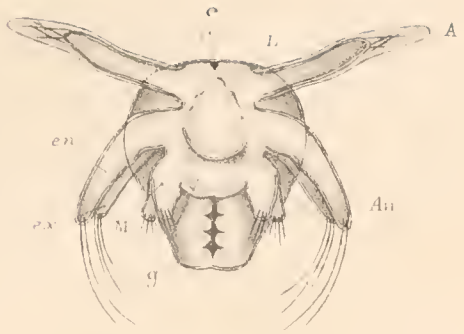
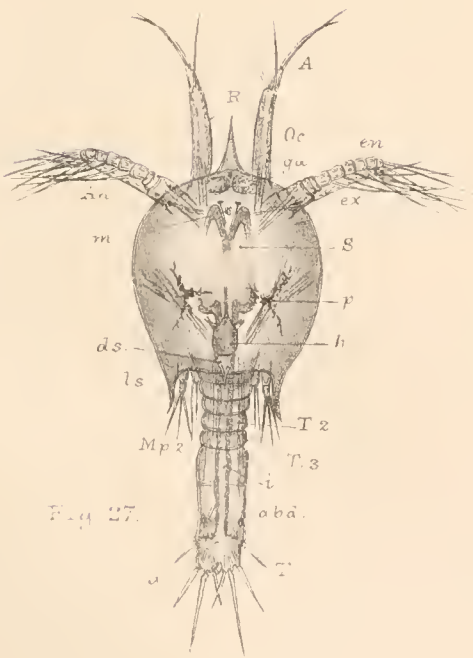



Fig. 24

Fig. 28

Fig. 29

Fig. 30

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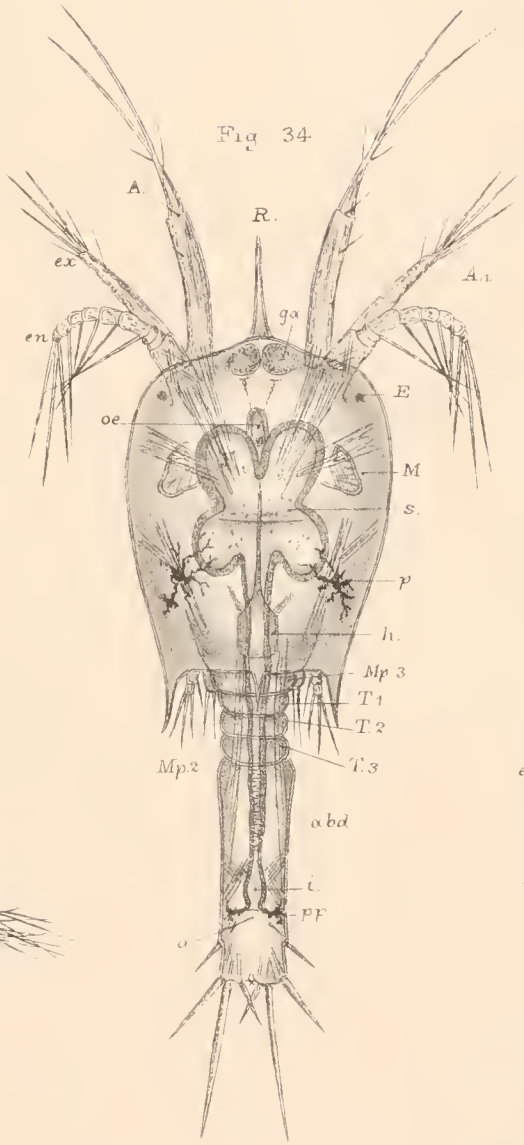



Fig. 34

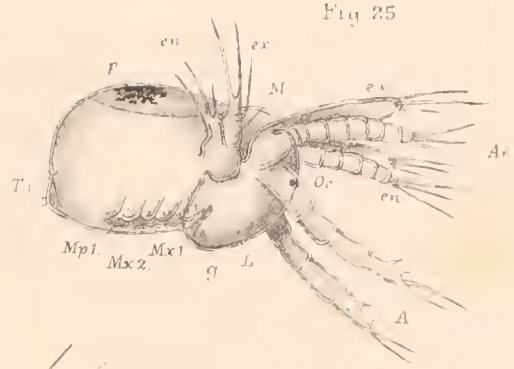



Fig 25

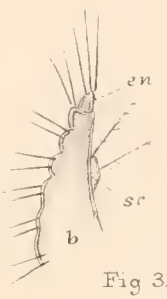



Fig 31

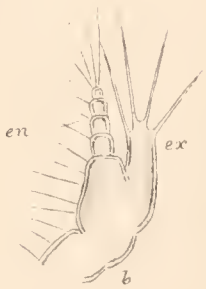



Fig. 32.

Fig. 33

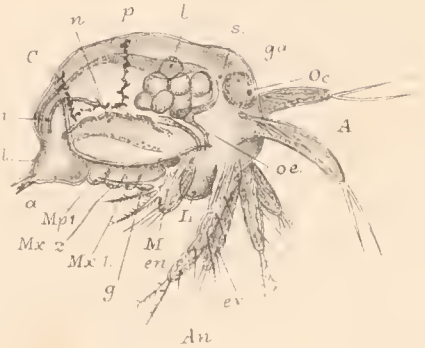



Fig. 26

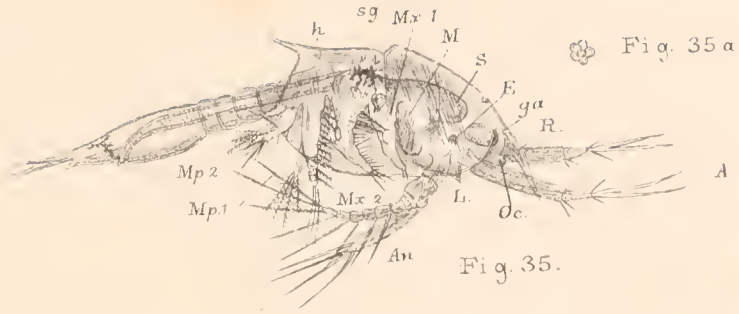
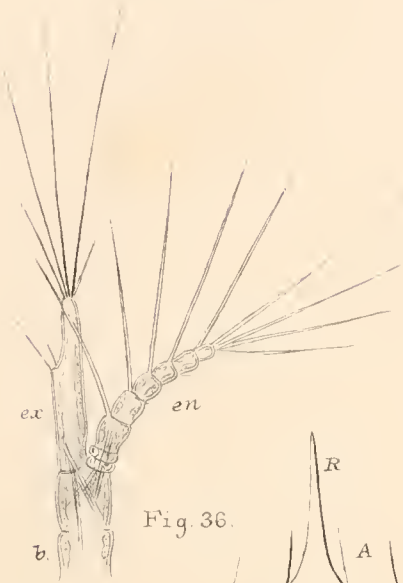



Fig. 35 a

Fig. 35.

Fig. 37.

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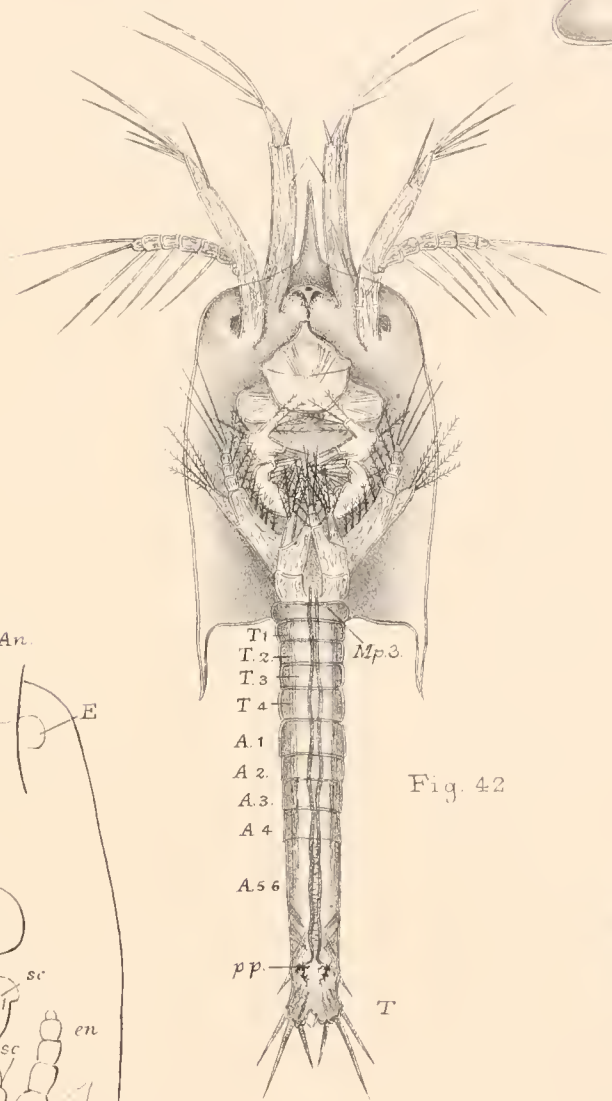



Fig. 42

Fig. 38.

Fig 42 a

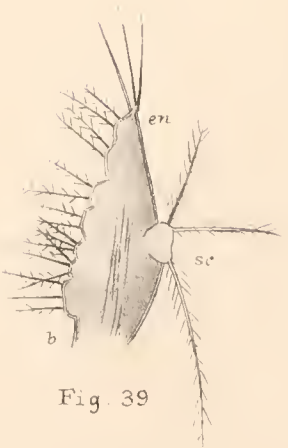



Fig. 39

Fig. 41.

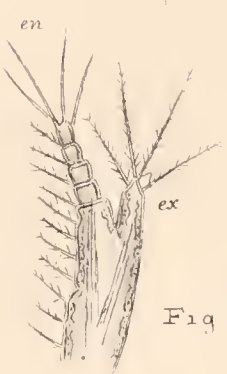
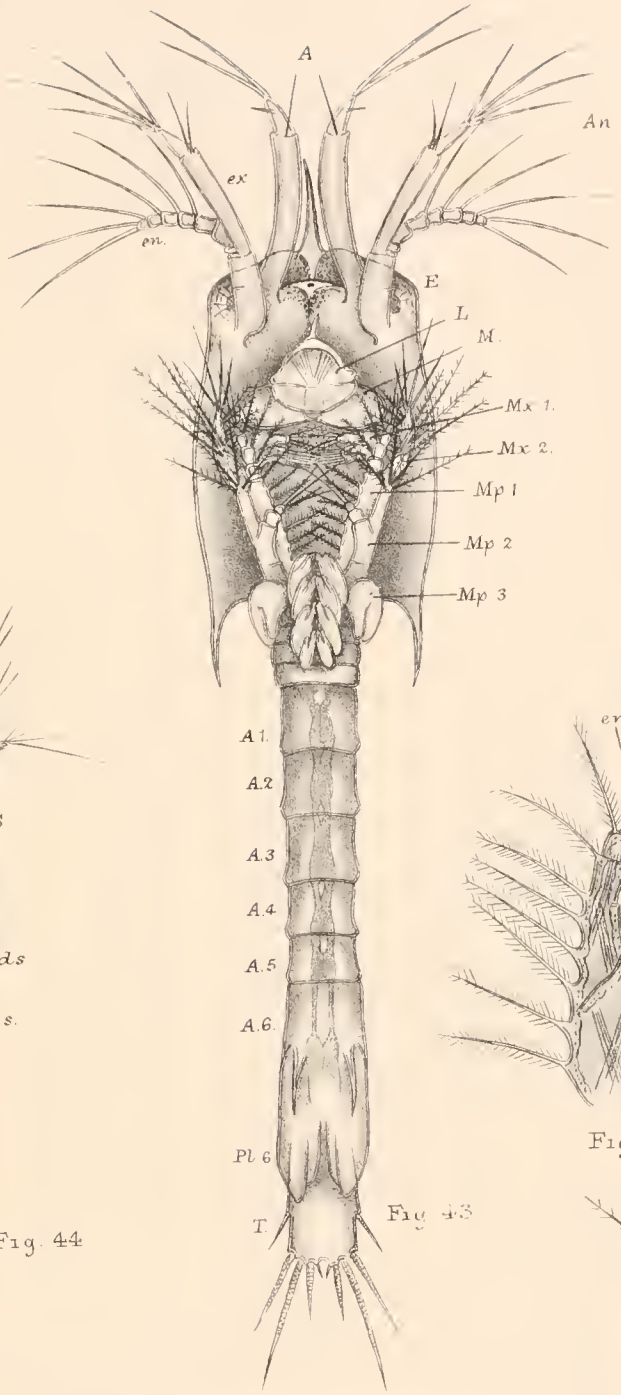



Fig 40

Fig. 46

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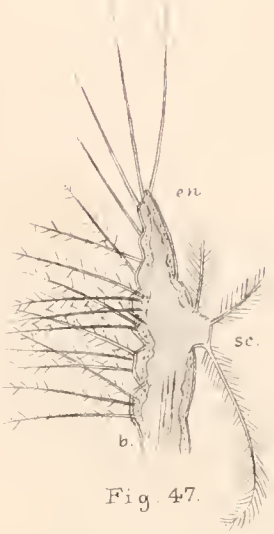


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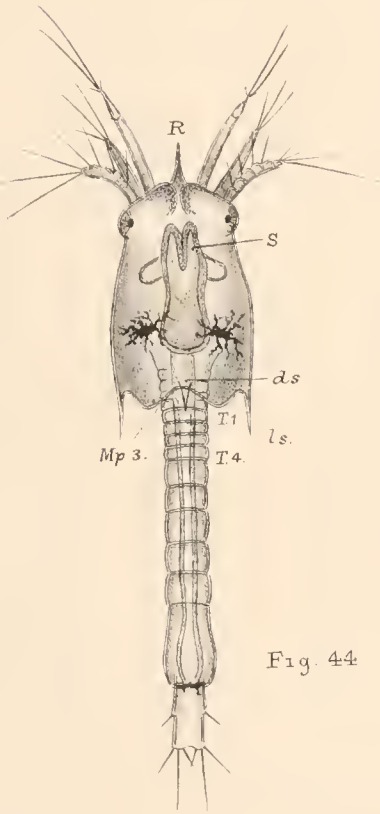


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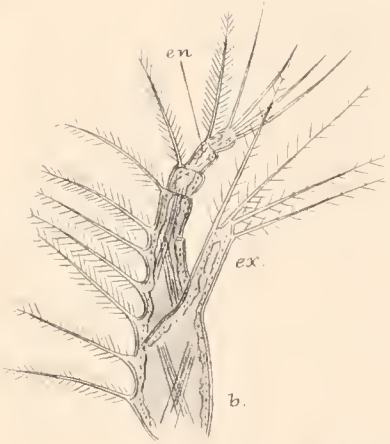


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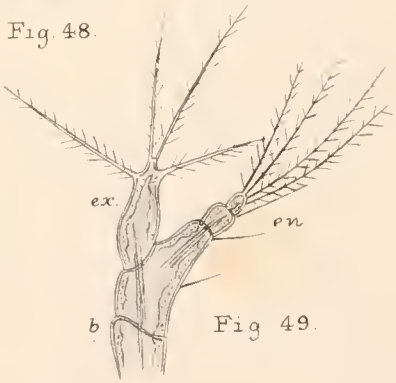


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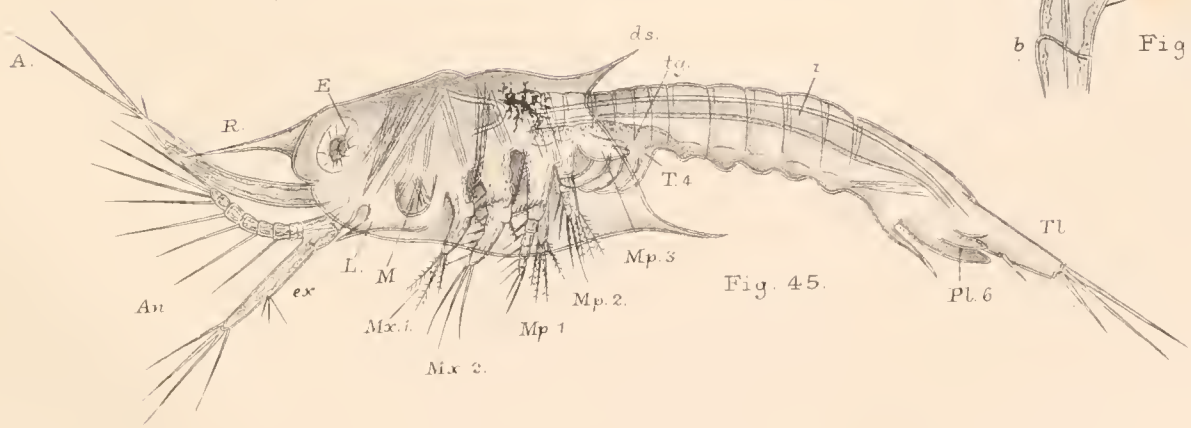



Fig. 45.

Fig. 54.

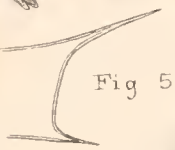


Fig 54a

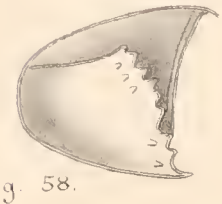


Fig. 58.

Fig. 59.

Fig 56.

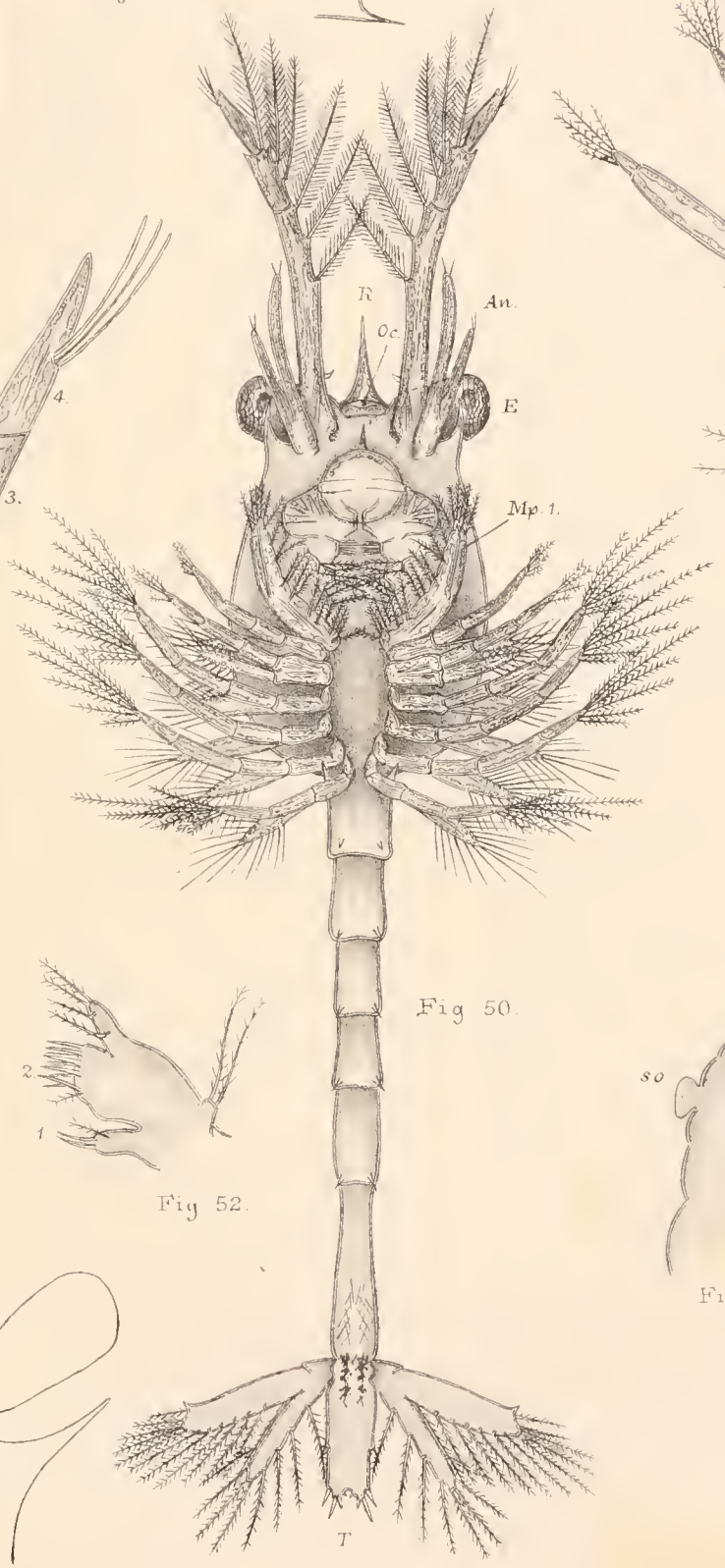



Fig 50.

Fig 51




Fig 52.

Fig. 53.

Fig 57

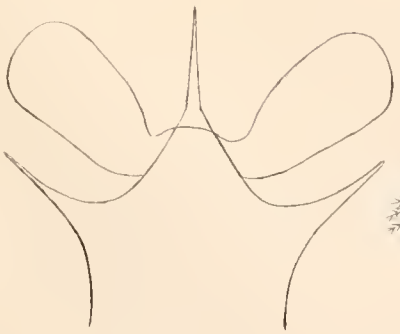


Fig 55.

Fig 60.

Fig 61

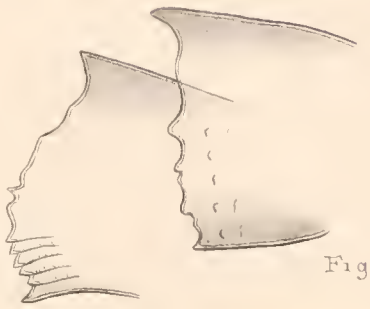


Fig 62

Fig. 63

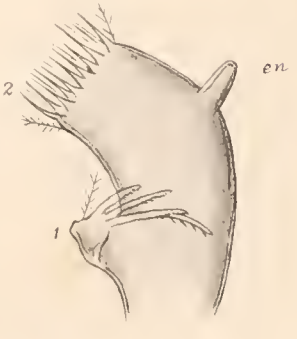



Fig 64



Fig 65

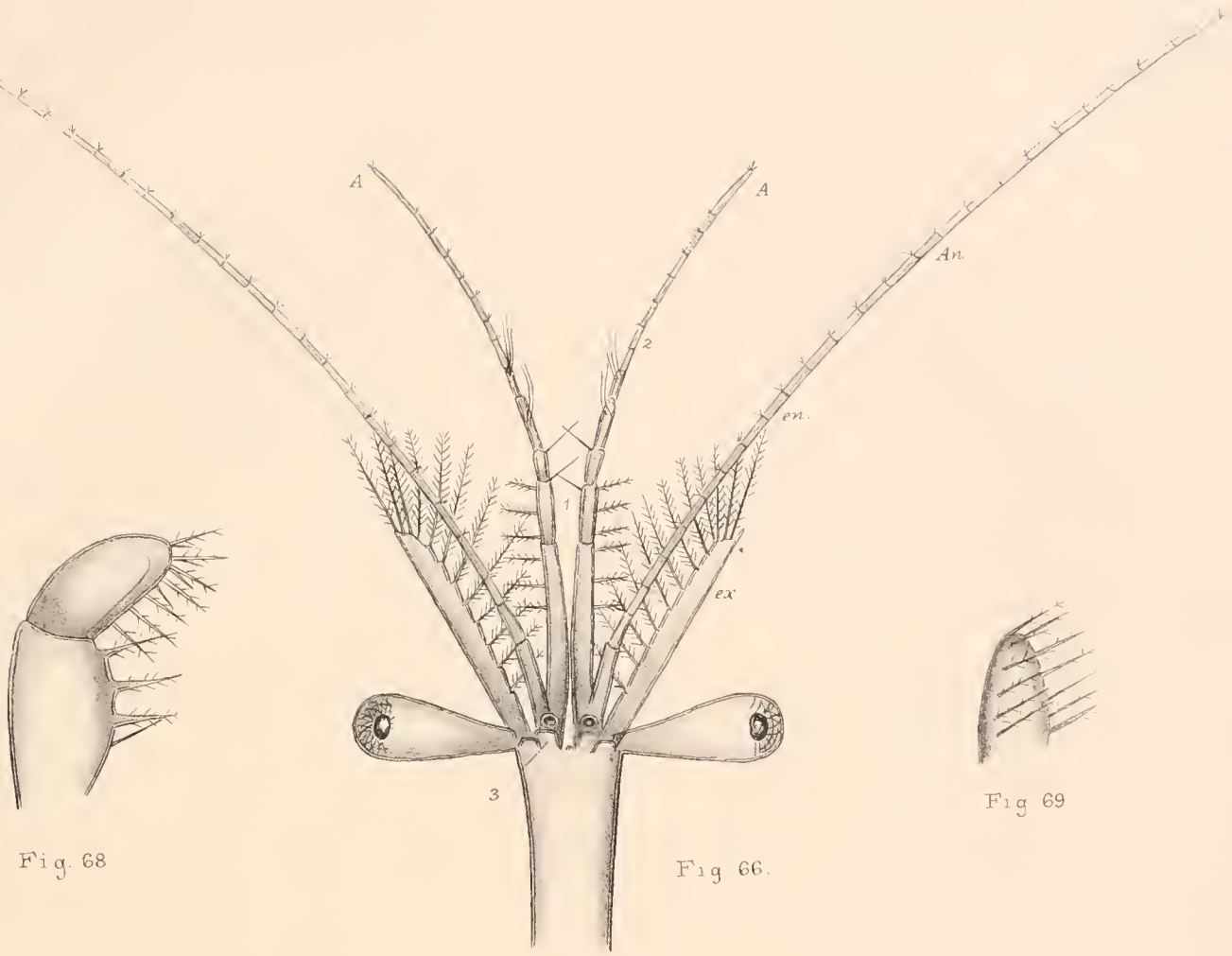


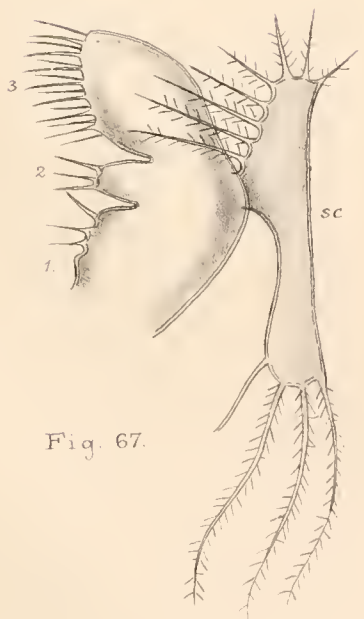

Fig. 66.



Fig. 68



Fig 69

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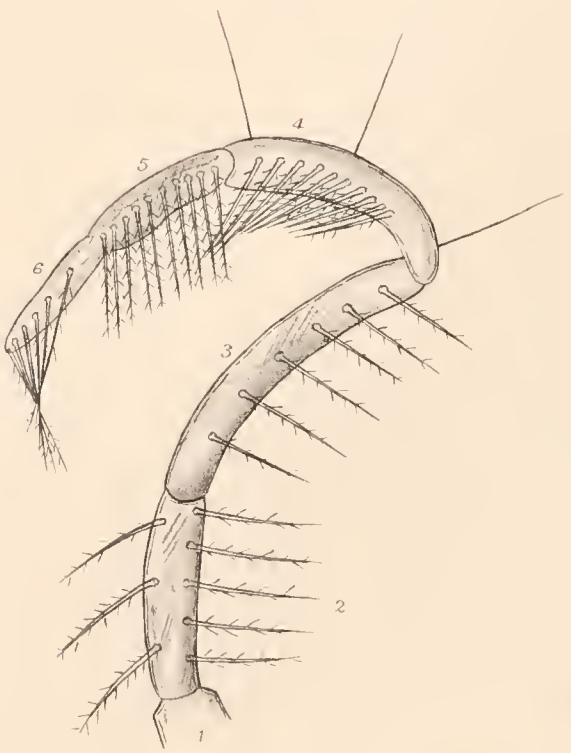


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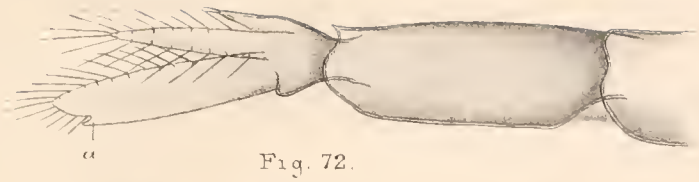



Fig. 72.

Fig. 73.

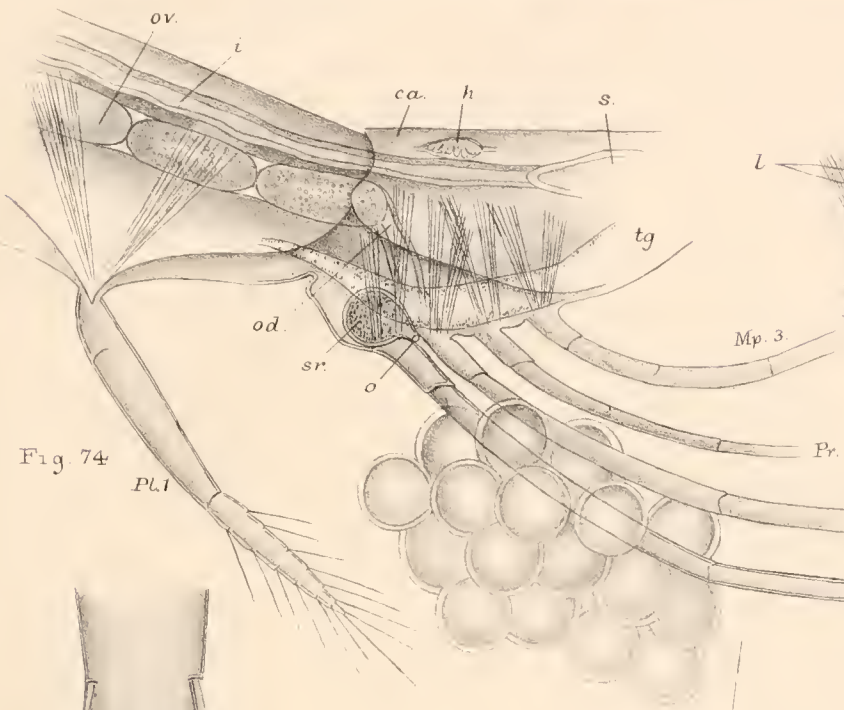



Fig 74

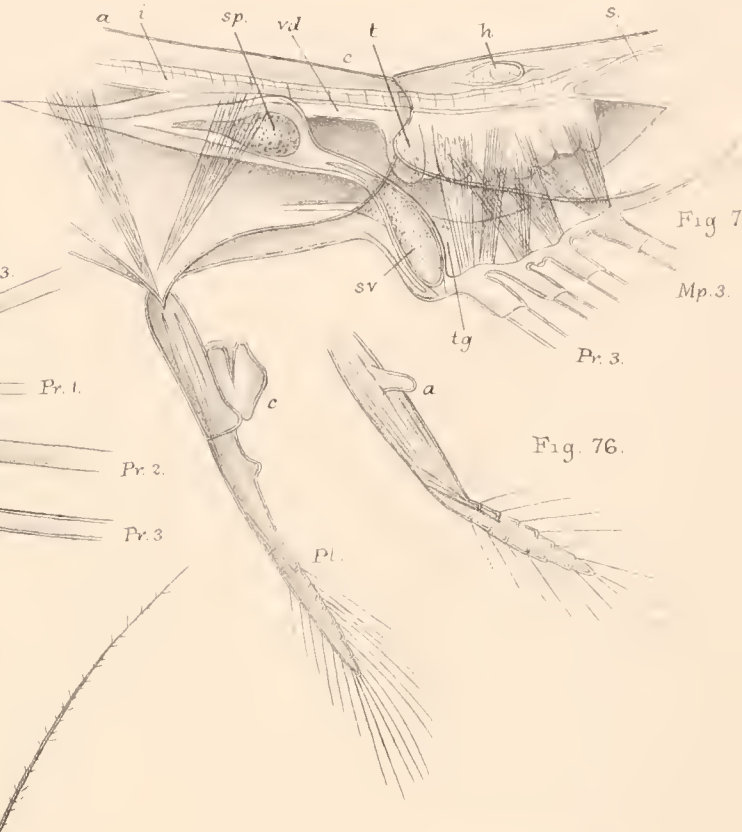



Fig 7




Fig. 76.

Fig 71.

Fig 81

Fig. 82.

Fig. 80.

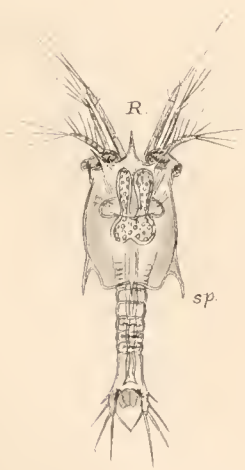



Fig. 79

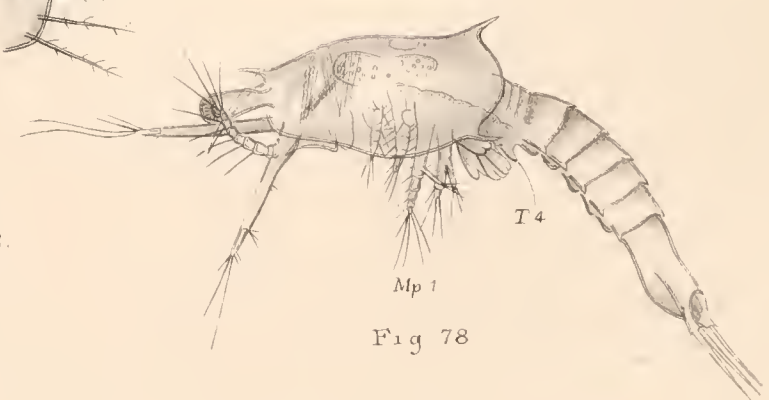



Fig 78

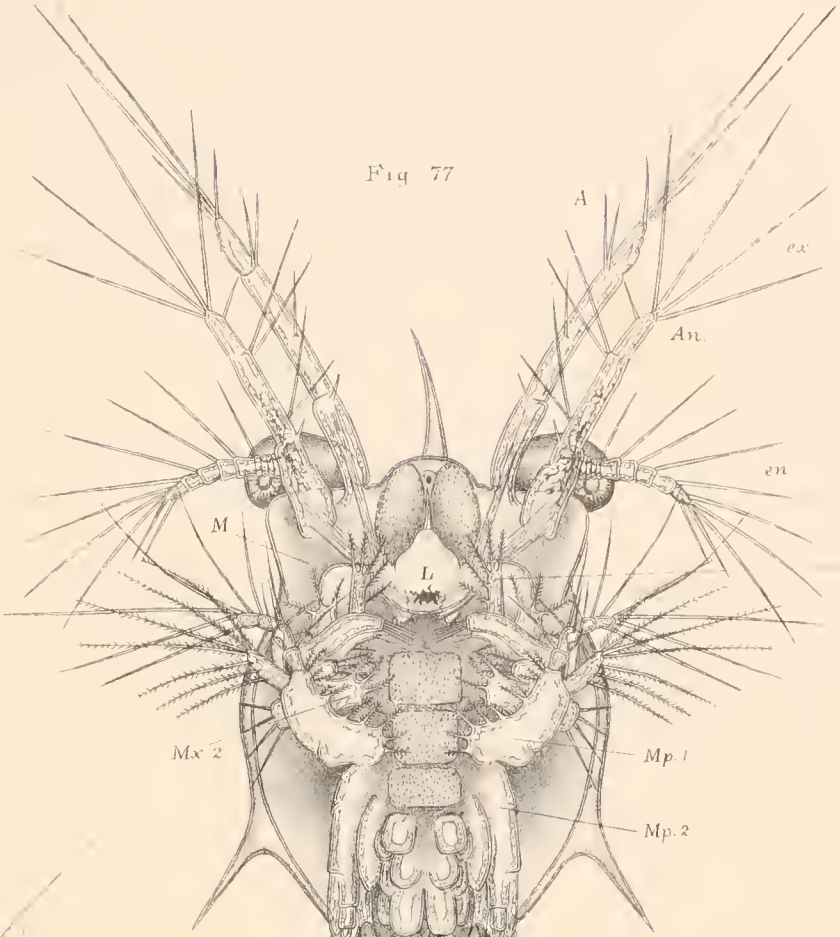
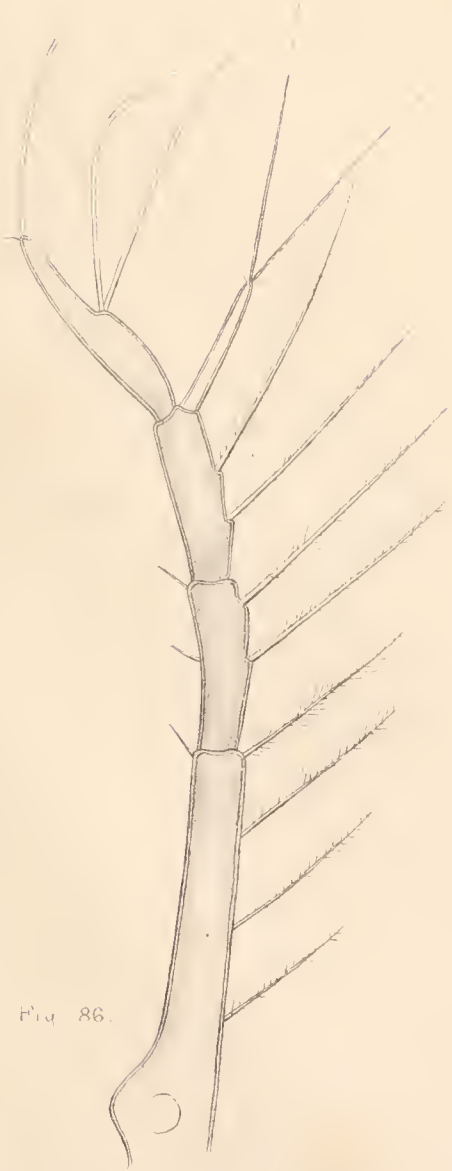



Fig 77



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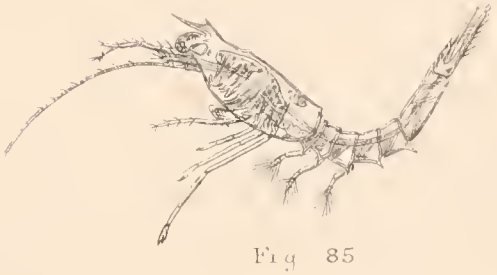
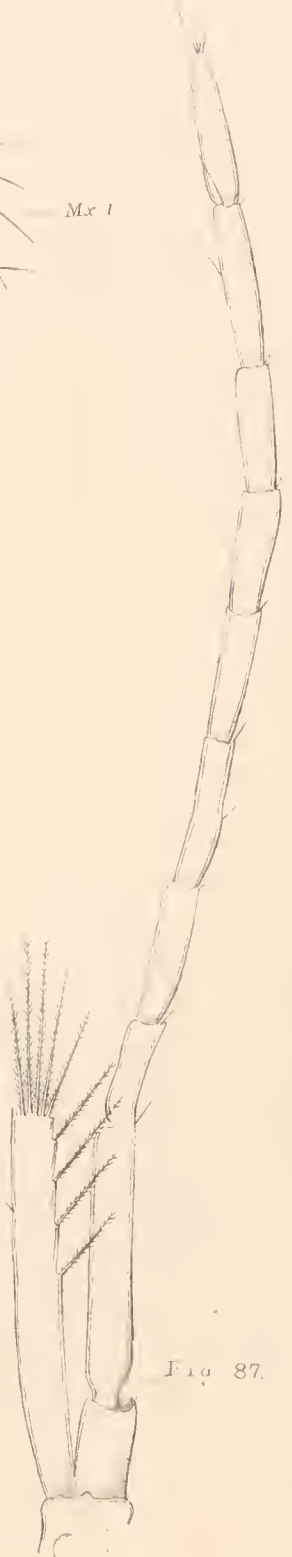


Fig 85



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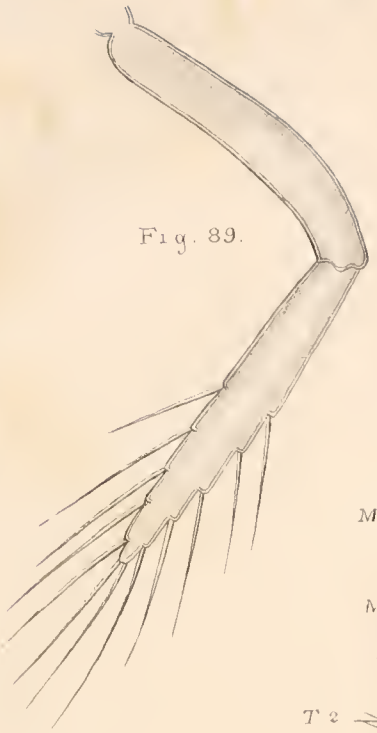

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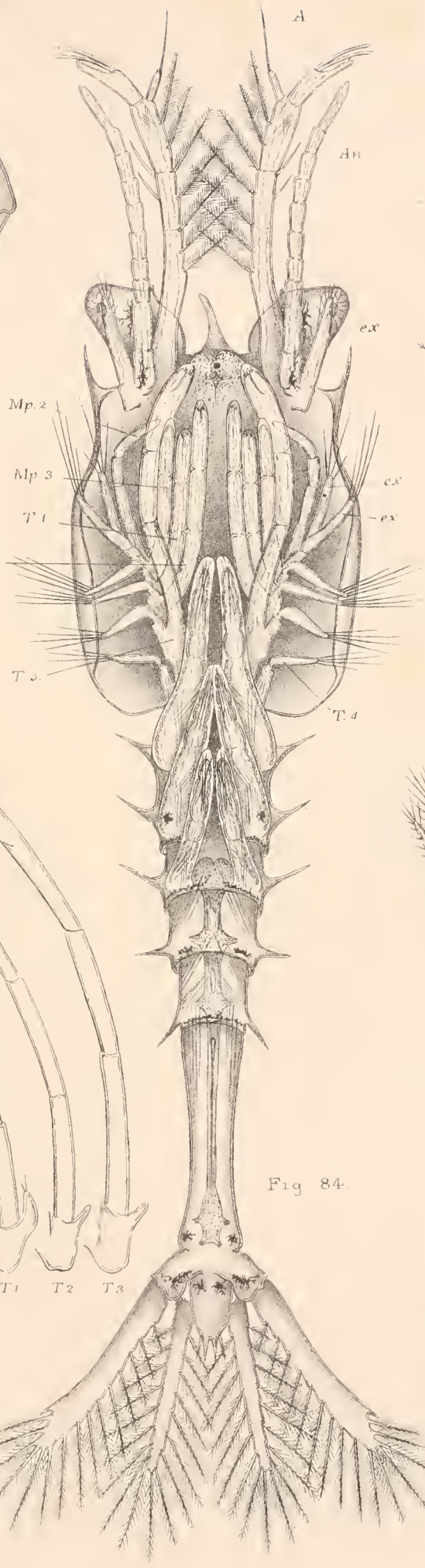


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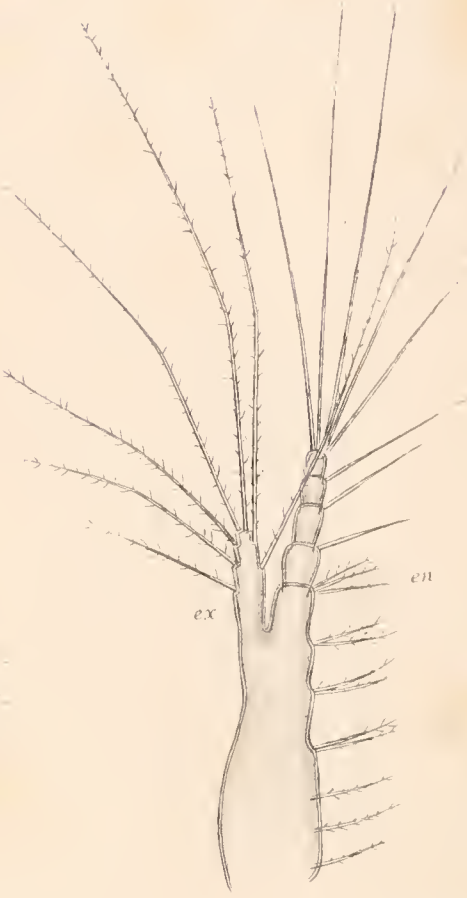


Fig 85

Fig 88

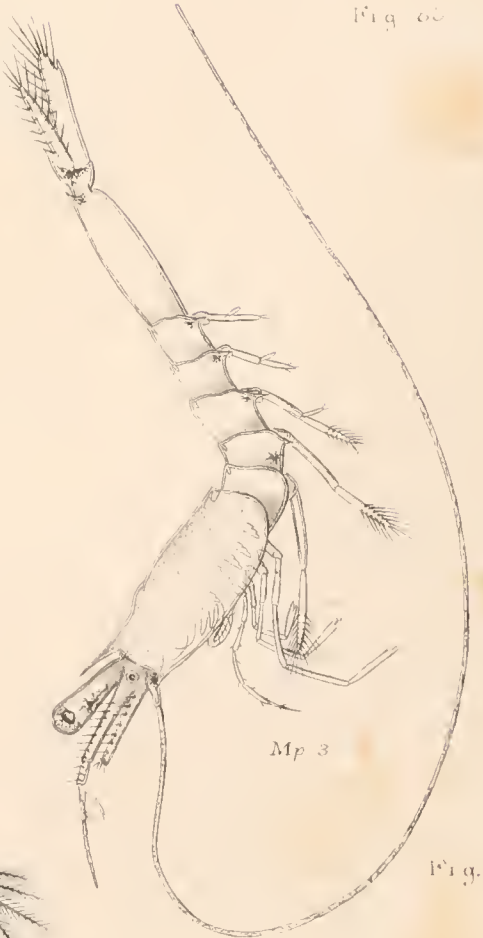


Fig. 90